
# From temperate to tropical seas: drivers of variation in reef-associated epifaunal invertebrate communities

by

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# STATEMENTS AND DECLARATIONS

## Declaration of Originality

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The research associated with this thesis did not required ethical approval on behalf of the University of Tasmania.

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Kate M. Fraser

Date: 24/6/2020

## Statement of Co-Authorship

The following people and institutions contributed to the publication of work undertaken as part of this thesis:

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- Doctor Rick D. Stuart-Smith, Institute for Marine and Antarctic Studies, UTAS – Supervisor
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## Papers included in this thesis and authors' roles:

Chapters 2-5 of this thesis have been prepared as scientific manuscripts for submission to peer-reviewed journals as identified on the title page of each chapter. In all cases the design and implementation of the research, data analysis, interpretation of results, and manuscript preparation was the responsibility of the candidate but was carried out in consultation with supervisors and other specialist contributors. The details of submission and co-author contributions are outlined for each chapter below.

### Paper 1, Taxonomic composition of mobile epifaunal invertebrate assemblages on diverse benthic microhabitats from temperate to tropical reefs

Reproduced in Chapter 2: this paper is published in Marine Ecology Progress Series

Kate M. Fraser, Rick D. Stuart-Smith, Scott D. Ling, Freddie J. Heather & Graham J. Edgar (2020) Taxonomic composition of mobile epifaunal invertebrate assemblages on diverse benthic microhabitats from temperate to tropical reefs. Marine Ecology Progress Series. 640:31-43. DOI: 10.3354/meps13295.

*Author Contributions*: KMF contributed approximately 60% to the planning, execution and preparation of work for the paper. KMF and GJE conceived the project. KMF conducted fieldwork, processed samples, analysed data and wrote the manuscript. GJE assisted sample identification. GJE and SDL received funding support and assisted with fieldwork and sample processing. FJH prepared data for, and assisted with, analysis. All authors contributed to methodology and edited the manuscript.

**Paper 2, Small invertebrate consumers produce consistent size spectra across reef habitats and climatic zones**

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**Paper 3, High biomass and productivity of epifaunal invertebrates living amongst dead coral**

Reproduced in Chapter 4: this paper is in review at Coral Reefs

Kate M. Fraser, Rick D. Stuart-Smith, Scott D. Ling & Graham J. Edgar (*in review*) High biomass and productivity of epifaunal invertebrates living amongst dead coral.

*Author Contributions*: KMF contributed approximately 85% to the planning, execution and preparation of work for the paper. KMF and GJE conceived the project. KMF conducted fieldwork, processed samples, analysed data and wrote the manuscript. GJE and SDL received funding support and assisted with fieldwork and sample processing. All authors contributed to methodology and edited the manuscript.

**Paper 4, Production of mobile invertebrate communities on shallow reefs from temperate to tropical seas**

Reproduced in Chapter 5: this paper has been accepted for publication in Proceedings of the Royal Society B: Biological Sciences

Kate M. Fraser, Jonathan S. Lefcheck, Rick D. Stuart-Smith, Scott D. Ling, Camille Mellin & Graham J. Edgar (*in press*) Production of mobile invertebrate communities on shallow reefs from temperate to tropical seas.

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# TABLE OF CONTENTS

# THESIS ABSTRACT

Globally, shallow reef ecosystems are undergoing dramatic changes, largely due to unprecedented climate change and exacerbated by local anthropogenic drivers. These changes are generally mediated by habitat transformation, which has critical implications for ecological communities and food web dynamics, often beginning at basal trophic levels with flow-on effects throughout food webs. Small mobile invertebrates ('epifauna') inhabiting the surfaces of structurally diverse reef habitats are prolific and ubiquitous on reefs worldwide, representing an essential basal trophic group that fuels much of shallow reef food webs.

This thesis examines the interactive influences of local and broad-scale drivers on epifaunal community composition, size structure and productivity on shallow reefs along a steep eastern Australian climatic gradient of 28.6° with mean annual temperature range of ~13°C. The overarching aim of this research is to understand how epifaunal communities vary across different reef habitat types, locations and latitudes, and environmental and ecological gradients, to better understand the broader ecological implications of ocean warming and local anthropogenic impacts on reef food webs.

Habitat is identified as the most important correlate of variation in epifaunal assemblages regardless of latitude or the metric used to quantify assemblages. Macroalgae, live coral and turfing algae represent three habitat extremes in terms of the taxonomic composition of epifaunal assemblages they host, with assemblage variation shaped by structural differences among habitats. The three habitat extremes also apply to the size structure and daily productivity of epifaunal assemblages, both important ecological properties with regards to the availability of this trophic group at a critical basal level in shallow reef food webs.

Despite distinct assemblage-habitat associations and the variation in dominant habitats across the latitudinal range studied – from cool-temperate macroalgae-dominated reefs to tropical coral reefs – daily community productivity of epifauna was largely invariant among sampling locations.

On subtropical to tropical reefs, dramatically different epifaunal assemblages were evident on live versus dead coral habitat, with dead coral supporting density, biomass, and daily productivity of epifauna 1 – 2 orders of magnitude higher than live coral. These distinctions between broadly classified coral habitats were consistent among four heterogenous subtropical and tropical reef locations. Epifaunal communities apparently represent an important avenue for ecological change associated with coral mortality through mass bleaching events.

Overall, my research strongly implies that habitat is the dominant driver of variation in reef-associated epifaunal assemblages. Broad-scale ocean warming and local anthropogenic stressors will likely influence changes to epifaunal assemblages on shallow reefs almost exclusively via transformation of habitats. The consistent trends across large biogeographic scales also suggest that accurate prediction of the basal food web resource provided by epifaunal invertebrates is possible when information on habitat distribution is available.

# Chapter 1

# GENERAL INTRODUCTION

Globally, shallow sunlit coastal reef ecosystems (≤40 m depth) are undergoing dramatic changes, largely associated with unprecedented ocean warming, and exacerbated by local threats such as pollution, habitat destruction, overfishing, and range-expansion of destructive species (Dulvy et al. 2003, Edgar et al. 2005, Ling et al. 2009, De'ath et al. 2012). Shallow reef systems are highly productive and important for human survival. For example, coral reef fish provide a critical source of protein and nutrients to many tropical communities (Cinner et al. 2013, Hicks et al. 2019), and macroalgae is a significant sink in the sequestration of carbon from our increasingly carbon-rich atmosphere (Krause-Jensen et al. 2018). Healthy reefs are also of great economic importance via industries such as commercial fishing and tourism (Bennett et al. 2015, Nash and Graham 2016).

On eastern Australia's tropical reefs, repeated events of coral bleaching and coral death are occurring (De'ath et al. 2012, Hughes et al. 2017b). Warming waters lead to coral bleaching as the symbiotic algae are expelled from coral tissue; when warming is prolonged corals cannot recover and skeletons become overgrown with turfing algae (Hoegh-Guldberg 1999). Increased frequency and intensity of tropical cyclones also threaten eastern Australia's coral reefs, with cyclone-driven seas breaking healthy and dead branching corals into extensive beds of turf-covered coral rubble (Cheal et al. 2017). A significant amount of coral loss in this region has also been attributed to the proliferation of crown of thorns seastar, a voracious coral predator (De'ath et al. 2012).

Eastern Australia's temperate reefs, historically dominated by macroalgae and giant kelp forests, are also changing, with warming water leading to kelp bed dieback and range

expansion of kelp-grazing sea urchins (Ling 2008, Johnson et al. 2011). These effects are exacerbated by increased sediment and nutrient loads (Irving and Connell 2002, Gorgula and Connell 2004). Informed and appropriate management and conservation of shallow reef ecosystems in this era of rapid change depends on comprehensive understanding of interactions between faunal and floral components, and the broader ecosystems they inhabit.

## Epifauna – an important, yet overlooked, trophic group

Despite extensive research on the ecology of shallow reef ecosystems, a thorough understanding of some critical components remains grossly under-developed. Field studies of shallow reef ecology often focus on highly visible taxa that can be quantified using underwater visual census, photographic or videographic methodologies. As a result, the ecology of reef fish communities has been extensively studied, more so than that of large mobile invertebrates, or sessile flora and fauna such as corals, sponges and macroalgae. The contribution of small biota – less than the body size reliably sighted in visual surveys – to shallow reef ecology is often overlooked.

Investigation of small mobile invertebrates (≤25 mm body size) living as epifauna (hereafter known as 'epifauna') on habitat-forming reef biota has historically been challenging due to these animals' small size, the immense diversity of their assemblages (assessable by only a small number of suitably skilled taxonomists), and their cryptic behaviour within structurally complex habitat (Taylor 1998). These small invertebrates are highly diverse, abundant and ubiquitous on shallow reef habitats, playing a crucial role in the flow of energy and cycle of nutrients within reef ecosystems (Taylor 1998, Kramer et al. 2014). Epifauna provide a major trophic pathway between primary producers (e.g. algae) and small carnivores (Edgar and Aoki 1993, Taylor 1998, Davenport and Anderson 2007), effectively channelling energy through shallow reef food webs. Thus, they are a prolific trophic group on both tropical and

temperate reefs and the dominant food source for many benthic invertivores (Kramer et al. 2015, Bates et al. 2017). Epifaunal assemblages also tend to be functionally diverse, including numerous detritivore, filter-feeder, and carnivore taxa. Assemblages are, however, typically dominated by herbivores reliant on small algal films and filaments (microphytobenthos) (Edgar 1993, Poore et al. 2012).

## Quantifying epifaunal assemblages

Given the trophic importance of epifauna for reef food webs, it is essential to quantify assemblages using metrics that demonstrate variation in their availability as a food resource. Taxonomic composition and diversity have been compared in several epifaunal studies, with most categorising animals at resolution no finer than family-level (Lewis and Anderson 2012, Marzinelli et al. 2016, Saarinen et al. 2018). This is due in part to the time-consuming nature of identifying small invertebrates to species-level (James et al. 1995), as well as a paucity of taxonomic information and expertise (Nakaoka et al. 2001). Family-level has, however, been shown to provide adequate information about the structure of small invertebrate assemblages in many situations, and is assessable by a much greater number of benthic ecologists (Warwick 1988, James et al. 1995, Wright et al. 1995, Karakassis and Hatziyanni 2000). Taxonomic composition of assemblages is a useful input to food web studies because of specific predation preferences amongst benthic invertivore taxa (Kramer et al. 2015, Soler et al. 2016).

Animal density, biomass and daily productivity within an assemblage provide useful metrics when assessing the overall quantity of food provided to the food web, and have been the focus of comparisons of epifauna under varying conditions (Edgar and Barrett 2002, Berthelsen et al. 2015, Cúrdia et al. 2015, Desmond et al. 2018). Patterns of benthic invertivory, however, are also highly dependent on invertebrate body size, with many benthic

invertivores demonstrating size selective predation (Edgar and Aoki 1993, Kramer et al. 2015). Ecological patterns in epifaunal assemblage size structure appear to be largely independent of taxonomic identity (Edgar 1983), and early studies in temperate regions identified a consistent log-linear relationship between invertebrate density and body size (Edgar 1993, Edgar and Aoki 1993, Edgar 1994). Nevertheless, assemblage size structure has rarely been considered in recent studies despite the fact that calculations of assemblage biomass and daily productivity require density by body size data (Edgar 1990b). Regardless, understanding the contribution of different sized epifauna to overall density, biomass and production of assemblages should be regarded as a necessary element if variation in food resources on shallow reefs is to be accurately estimated.

## The importance of habitat structure

Ecological research involving small epifaunal invertebrates has largely focused on relationships between assemblages and the structure of their immediate habitat, with the majority of studies conducted at local scales. The physical structure of habitat has long been known as a strong correlate of variation in faunal assemblage parameters such as taxa richness, biomass, and total abundance in benthic marine ecosystems (Luckhurst and Luckhurst 1978, Hicks 1985, Caley and St John 1996, Gratwicke and Speight 2005, Hunter and Sayer 2009). Quantifying the structure of habitat depends on, and must be appropriate for, the size scale of fauna in question (Nash et al. 2013). For epifaunal invertebrates habitat samples are generally ≤1L volume with structure quantified at submillimetre – centimetre scales (Kramer et al. 2017). Comparisons of multiple macroalgal taxa (Marzinelli et al. 2014) and coral taxa (Stella et al. 2010) with different structural characteristics (e.g. complexity, maximum length, diameter, inter-branch space; (Stella et al. 2010, Marzinelli et al. 2014)) have revealed taxonomically distinct epifaunal assemblages associated with each habitat-forming taxon. Density, biomass, productivity and size structure of epifaunal assemblages

may also correlate with different structural metrics of the immediate habitat (Edgar 1990a, 1994, Edgar et al. 1994, Taylor 1998, Kramer et al. 2014, Kramer et al. 2017). Understanding the local scale relationship between assemblages of epifauna and the structure of their habitat is critically important as reef habitats transform under conditions of climate change and local anthropogenic impacts.

## Interactions between habitat and environmental and ecological processes

Environmental and ecological covariates may interact with habitat-epifaunal relations across local, regional and global scales, influencing the way assemblages vary among habitats. In other faunal communities, biotic factors such as competition or predation (Almany 2004a, Almany 2004b) interact with habitat effects. Human influence can also significantly affect the structure of faunal assemblages. Fishing pressure, for example, has been shown to impact fish and larger invertebrate assemblages that strongly depend on habitat structure (Alexander et al. 2009, Cinner et al. 2013). Environmental covariates such as temperature can influence both faunal assemblages and habitat structure via mechanisms such as seasonality (Nakaoka et al. 2001) and depth (Trebilco et al. 2015). Latitude and climatic zone can represent broad gradients in temperature, as well other processes such as primary production and predation pressure, that may interact with habitat-faunal relations through a diversity of mechanisms. Understanding the interactive effects of habitat and the environmental and ecological gradients inherent with latitude on reef food web dynamics is critical for predicting changes resulting from habitat transformation and ocean warming. Ecological studies of reef systems across broad latitudinal gradients have involved fishes (Floeter et al. 2005), large mobile invertebrates (Stuart-Smith et al. 2018), macroalgae (Wismer et al. 2009) and corals (Harriott and Banks 2002), yet to date minimal research has investigated multiple drivers and interactive effects with habitat structure on the ecology of epifaunal invertebrate communities.

## Latitudinal patterns at biogeographic scales

From the limited research comparing epifaunal assemblages among latitudinally widespread locations, one cannot easily draw clear and consistent conclusions. One early study identified latitude as a highly inconsistent predictor of the diversity, density and size of seagrass-associated epifauna (Virnstein et al. 1984). Another early study demonstrated constant daily productivity of epifauna on structurally uniform artificial habitats among widespread locations but clear latitudinal patterns of variation in abundance, biomass and size structure (Edgar 1993). More recently, Kramer et al. (2017) investigated assemblage parameters of small benthic crustaceans on selected reef habitats representing a gradient of structural complexity, providing comparisons between one tropical and one temperate location. They identified significant relationships between crustacean assemblages and both habitat complexity and climatic zone. The question remains whether patterns exist for shallow reef epifauna across an extensive latitudinal gradient, and how such patterns interact with epifauna-habitat relationships. As yet, no published research has investigated variation in shallow reef epifaunal assemblages among structurally heterogenous habitats along a temperate to tropical latitudinal gradient. It is unknown whether the influences of habitat and latitude interact at biogeographic scales broader than two disparate locations, whether inclusion of taxa additional to crustaceans change observed relationships, or how size-based assemblage metrics respond to habitat/latitude interactions. Answering these question may provide crucial information for predicting how this basal epifaunal food source will shift in response to the direct and indirect effects of a changing global climate, combined with increasing local anthropogenic stressors.

## 1.1 Thesis aims

In the context of available literature, I aimed to assess the interactive effects of habitat and latitude on assemblages of epifaunal invertebrates (0.125 – 22 mm body size) within eastern Australian shallow reef ecosystems. Specifically, this research sought to answer the following questions, with investigations relevant to each question presented in the ensuing four chapters:

(1) How does the taxonomic composition of epifaunal assemblages vary among structurally and taxonomically diverse benthic habitat types along a temperate to tropical latitudinal gradient? (Chapter 2).

(2) How do latitude and habitat interact to influence variation in the size structure of epifaunal assemblages? (Chapter 3).

(3) How do different epifaunal taxa and body size classes contribute to assemblage variation associated with live and dead coral habitats on subtropical to tropical reefs? (Chapter 4).

(4) What are the major environmental and ecological drivers of the daily productivity provided by epifaunal assemblages to shallow reef food webs? (Chapter 5).

To answer these questions, I collected epifaunal invertebrates via SCUBA by sampling replicates of 21 structurally diverse benthic microhabitats from 71 shallow reef sites within 12 distinct locations. Locations spanned a broad biogeographic range along the eastern seaboard of Australia, from cool temperate southern Tasmania (43.3°S) to the tropical northern Great Barrier Reef (14.7°S). While the availability of microhabitats varied among locations, I attempted to sample all microhabitats available within each.

For each sample, I removed epifauna from their habitat, identified and size fractionated assemblages, then quantified them according to taxonomic composition, size structure, and

overall density, biomass and daily productivity. All chapters of this PhD thesis were led, analysed and written by myself, with the support of my supervisors. All four analytical chapters have been submitted to peer-reviewed journals with my supervisors as co-authors. A concatenated list of literature cited throughout the six chapters of this thesis can be found on page 142.

# Chapter 2

## TAXONOMIC COMPOSITION OF MOBILE EPIFAUNAL INVERTEBRATE ASSEMBLAGES ON DIVERSE BENTHIC MICROHABITATS FROM TEMPERATE TO TROPICAL REEFS

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**Preface:**

*This work has been published in a refereed journal and is presented below in identical form. The citation for the original publication is:*

Fraser KM, Stuart-Smith RD, Ling SD, Heather FJ, Edgar GJ (2020) Taxonomic composition of mobile epifaunal invertebrate assemblages on diverse benthic microhabitats from temperate to tropical reefs. Marine Ecology Progress Series. 640: 31-43. DOI: 10.3354/meps13295

In Chapter 2 I compare the family composition of macro-epifauna (≥1 mm body size) among microhabitats across the entire biogeographic range from which samples were collected. Chapter 2 links to Chapters 3, 4 and 5 by introducing strong microhabitat associations and identifying which microhabitats host notably disparate assemblages of epifauna (i.e. extremes).

## 2.1 Abstract

Anthropogenic drivers are flattening reef structure from three-dimensional habitats composed of macroalgae and live branching corals towards low-profile turfing algae. Our current understanding of the consequences of widespread reef degradation currently fail to consider the responses of small mobile invertebrates ('epifauna') to patterns of change amongst reef structural elements ('microhabitats'). Here, the taxonomic composition of 152 epifaunal assemblages was compared among 21 structurally diverse benthic microhabitats across an Australian temperate to tropical climatic gradient, spanning 28.6 degrees in latitude from Tasmania to the northern Great Barrier Reef. Epifauna varied consistently with different microhabitat types, and to a much lesser extent with latitude. Macroalgae, live branching coral, and turfing algae represented three extremes for epifaunal community structure – most microhabitats possessing epifaunal assemblages intermediate between these endpoints. Amongst structural characteristics, epifauna related primarily to the degree of branching and hardness of microhabitats. Mobile invertebrate communities are likely to transform in predictable ways with collapse of large erect macroalgae and live coral towards low-lying turf-associated communities.

## 2.2 Keywords

macrofauna, habitat structure, coral, macroalgae, turf

## 2.3 Introduction

In an era of rapidly changing climate, reef habitats are undergoing significant transformation. Coral reefs are bleaching and corals that do not recover are overgrown with turfing algae and eventually break down into turf-covered rubble (Nelson et al. 2016, O'Brien and Scheibling 2018). Macroalgae also sometimes succeed coral loss (Mumby et al. 2007b). On temperate

reefs, kelps and other large macroalgae are declining in many regions due to warming water and associated invasion of prolific herbivores (Ling et al. 2009, Vergés et al. 2014, Krumhansl et al. 2016), as well as increased sediment and nutrient loads (Irving and Connell 2002, Gorgula and Connell 2004). Turfing algae often succeed macroalgae (Filbee-Dexter and Wernberg 2018, O'Brien and Scheibling 2018, Reeves et al. 2018). The terms 'turf' and 'turfing algae' here refer to dense or matted fine filamentous algae ≤ 2 cm high with minimal sandy sediment entrapped by thalli (Connell et al. 2014) (Table 2.1). 'Macroalgae' refers to larger algal species, further categorised and described in Table 2.1. Coral, macroalgae and turf are structurally distinct habitats; transitions in their local dominance can represent a discontinuous phase-shift in reef state (Ling et al. 2015, Hughes et al. 2018), which may flow-on to significantly alter associated faunal assemblages.

Despite dramatic changes in habitat-forming species, very little is known about consequential effects on associated organisms, including epifaunal invertebrates ('epifauna'). Given the crucial secondary production role of small mobile invertebrates in reef food webs (Taylor 1998), changes to epifaunal communities can potentially cascade to affect fish production and ultimately human wellbeing. Kramer et al. (2014) observed distinct assemblages of small crustaceans when comparing live branching coral with dead coral and coral rubble. Similarly, huge shifts in epifauna are observed during the loss of kelp beds from temperate reefs (Ling 2008), and significantly different assemblages of epifaunal crustaceans have been described in association with macroalgae and algal turf (Kramer et al. 2017). Understanding the differences in epifaunal assemblages associated with live coral, macroalgae and turf, as well as other, less dominant, reef-associated habitats ('microhabitats'), is critically important in the context of changing reef ecosystems (Ling et al. 2018a).

Small mobile invertebrates living as epifauna play a key role in nutrient cycling within reef ecosystems (Edgar and Aoki 1993, Taylor 1998, Davenport and Anderson 2007), providing

the critical initial trophic link between benthic primary production and secondary carnivores such as decapod crustaceans and fishes (Edgar and Shaw 1995, Duffy and Hay 2000, Nakaoka et al. 2001, Newcombe and Taylor 2010, Kramer et al. 2013, Tano et al. 2016). Despite their importance in food webs, mobile epifaunal invertebrates are a relatively poorly studied group of animals, largely due to sampling challenges associated with their small size, immense diversity, and cryptic behaviour within structurally complex habitats (Taylor 1998). Small biota < 1 cm body-size are especially poorly understood as they are below detection limits when visual, videographic and photographic survey methods are used (Romero-Ramirez et al. 2016). The relationships between reef-associated epifaunal assemblages and the function and morphology of their associated microhabitats are still largely unknown.

Ecological research involving small epifaunal invertebrates has primarily focused on relationships between assemblages and the structural characteristics of their immediate habitat (MacArthur and MacArthur 1961, Kovalenko et al. 2012). At a local scale, microhabitats of different structure support different epifaunal assemblages (Hacker and Steneck 1990, Gee and Warwick 1994a, Chemello and Milazzo 2002, Stella et al. 2010, Kramer et al. 2014, Marzinelli et al. 2014, Stelling-Wood et al. 2020). Comparisons of multiple macroalgal taxa (Hacker and Steneck 1990, Gee and Warwick 1994a, Chemello and Milazzo 2002, Marzinelli et al. 2014) and coral taxa (Stella et al. 2010, Kramer et al. 2014) with different structural characteristics (e.g. complexity, maximum length, diameter, inter-branch space, branch width and length) have revealed taxonomically distinct epifaunal assemblages associated with each habitat-forming taxon. These results suggest different epifaunal taxa have different requirements with regards to habitat structure and, as such, habitat structure is a major driver of faunal assemblage composition (Taylor and Cole 1994).

Epifauna-habitat research has primarily been conducted using data from single sampling locations, thus the effects of the large-scale environmental variation from temperate to

tropical coasts on epifaunal relationships with habitat structure are not well known. Latitudinal variation has been identified in other marine faunal assemblages, from estuarine infauna (Attrill et al. 2001) to reef fishes (Floeter et al. 2004). Kramer et al. (2017) found distinct epifaunal assemblages associated with similarly complex habitats at a tropical and a temperate reef location. In contrast, Bergen et al. (2001) found that latitude did not significantly contribute to variation in infauna assemblages among habitats of different sediment size. To date, no studies have investigated the composition of epifaunal assemblages in association with structurally diverse benthic habitats across a temperate to tropical latitudinal gradient. In order to effectively predict epifaunal variation in shallow reef systems it is important to understand whether latitudinal changes override the effect of habitat structure, or if habitat structure at the scale appropriate to small invertebrates is a more dominant correlate of community composition.

Here we investigate relationships between epifaunal assemblages and reef microhabitats across 12 locations spanning the eastern seaboard of Australia from southern Tasmania (43.3° S) to the northern Great Barrier Reef (14.7° S). Epifaunal invertebrates were collected in association with 21 microhabitats that were widespread across this biogeographical scale – a diversity of macroalgae, coral, and turfing algae microhabitats, as well as sponges and seagrass growing on sand patches amongst broken reef. The nationally-applied CATAMI (Collaborative and Automated Tools for Analysis of Marine Imagery; (Althaus et al. 2015)) classification scheme was used as a basis from which to define reef-associated microhabitats according to taxonomic and functional differences in structure (Table 2.1).

Specifically, we asked the questions: (1) how does the taxonomic composition of epifaunal assemblages vary among microhabitats across a broad temperate to tropical latitudinal gradient? and (2) which microhabitat structural characteristics correlate most strongly with variation in assemblage composition?

## 2.4 Materials and methods

### 2.4.1 Study area and field sampling

A total of 152 samples of reef-associated benthic microhabitats and associated epifauna were collected from 12 locations spanning 28.6 degrees in latitude along the eastern seaboard of Australia, from southern Tasmania (43.3°S) to Lizard Island in the northern Great Barrier Reef (14.7°S) (Fig. 2.1). Sampling was conducted in September and October 2015, and over a two-year period from January 2017 to November 2018. Samples were collected at depths of 1–14 m, depending on the depth of accessible reef.

At each location, between 2 and 11 sites were sampled, separated by a minimum distance of 2.5 km. Site and sample numbers depended on accessibility of reef and the timing of each sampling trip. Sampling involved SCUBA-based collection of 21 microhabitats varying in taxonomy, morphology and functionality (Table 2.1; Table 2.5 (S1)). Microhabitats were categorised by coarse taxonomic and functional differences in structure. Each sample involved concurrent collection of a microhabitat and associated epifaunal invertebrates. Microhabitats were selected for sampling as they were sighted, providing samples were at least 5 m from each other. To avoid spatial confounding within site that could arise if microhabitats were each clustered in few locations, microhabitats were generally sampled only once at any given site to ensure data were fully independent. However, when natural availability of microhabitats constrained this approach, epifaunal data from replicate samples were averaged such that one set of data was produced for each microhabitat within a site.

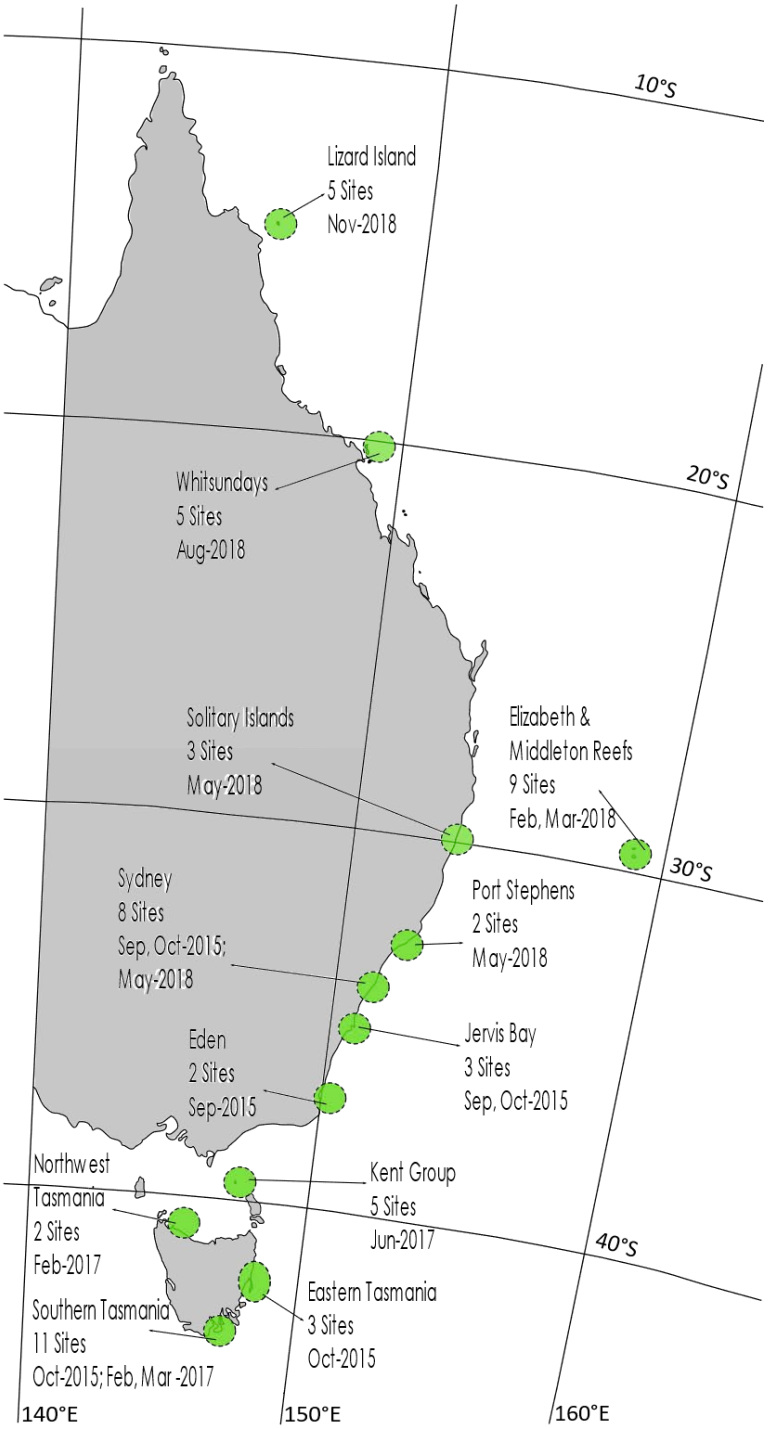



**Fig. 2.1** Map of eastern Australia showing sampling locations, number of sites and the date range of field collections.

**Table 2.1** Microhabitats sampled, with code used in figures below, brief physical description, and example genera.

| Microhabitat category | Code | Description | Example genera |
|---|---|---|---|
| Large brown laminarian kelps | Lam | Large habitat forming, overstorey kelp, wide lamina | *Ecklonia* |
| Fucoid algae | Fuc | Robust, vertical, complex-branching brown algae, leafy appearance | *Sargassum, Xiphophora, Acrocarpia, Cystophora* |
| Small to medium foliose brown algae | Bfol | Sheet-like, soft plate-like, or filamentous brown understorey algae | *Zonaria, Dictyota, Padina, Lobophora, Halopteris* |
| *Caulerpa* | Caul | Green algae of genus *Caulerpa*, thick vertical growth (often finely branching) from horizontal stolon | *Caulerpa* |
| Green calcified algae | Gcal | Green algae, branching into calcified segments, vertical growth habit | *Halimeda* |
| Foliose green algae | Gfol | Thin sheet-like, thick branching, or filamentous green algae, vertical growth habit | *Ulva, Codium, Chlorodesmis, Chaetomorpha* |
| Foliose red algae | Rfol | Flexible red algae, branched or leafy, vertical growth habit | *Plocamium, Gracilaria, Pterocladia, Acathophora, Laurencia* |
| Geniculate coralline algae | GCA | Red calcified algae, fine branches jointed or segmented, vertical growth habit | *Corallina, Amphiroa* |
| Turfing algae | Turf | Fine filamentous turfing algae ≤ 2 cm high growing densely or matted on hard substrate, with minimal sandy sediment entrapped | *Feldmannia, Polysiphonia* |
| *Halophila* | Halo | Seagrass with soft ovate leaves often stalked in pairs from horizontal stolon half buried in sediment immediately adjacent to reef | *Halophila* |
| Sponges, encrusting | SpE | Sponges forming a crust over substrate | *Mycale, Aplysilla, Tedania, Chondrilla* |

| | | | |
|---|---|---|---|
| Sponges, erect | Spo | Erect sponges rising from substrate; colony height greater than width; appears solid in cross-section | *Halichondria*, *Echinoclathria*, *Ancorina* |
| Hydrocoral | Hcol | Branching or foliaceous erect colonies | *Millepora* |
| Soft coral | Soft | Semi-erect, lobed soft corals | *Lobophytum*, *Sarcophyton*, *Xenia* |
| *Pocillopora* | Pocil | Stony corals forming branched colonies, genus *Pocillopora* | *Pocillopora* |
| Branching *Acropora* | BrAc | Stony, branching corals forming colonies, genus *Acropora* | *Acropora* |
| Tabular *Acropora* | Tab | Stony branching corals forming tabular colonies | *Acropora* |
| Massive coral | Mas | Slow-growing, massive, small polyp stony corals | *Porites*, *Favia* |
| Other branching/erect coral | Bra | Fine or robust branching, columnar or foliaceous stony coral colonies | *Porites*, *Turbinaria*, *Seriatopora*, *Stylophora* |
| Dead coral | Dead | Dead erect coral skeleton overgrown with fine filamentous algae | *Acropora (dead)*, *Pocillopora (dead)* |
| Coral rubble | Peb | Broken dead coral rubble overgrown with turfing algae | *Acropora (dead)*, *Pocillopora (dead)*, *Porites (dead)* |

Prior to collection, a 25 cm x 25 cm grid-subdivided quadrat was placed over the selected microhabitat and photographed to quantify the planar area of the microhabitat. Branching hard corals were chiselled off the reef; soft corals, sponges, seagrass and macroalgae were removed with a sharp knife; coral rubble was collected by hand. These samples were enclosed immediately and sealed within plastic bags. Epifauna associated with massive corals and turfing algae, which could not easily be removed for sampling, were collected using an underwater venturi-powered vacuum with a 500 µm mesh bag secured over the outlet. The

mesh bag was removed after sampling and placed in a plastic bag to retain small animals. The entire planar area within the 25 cm x 25 cm quadrat was swept in suction samples.

Epifaunal invertebrates were taken to the surface and preserved in the field before transportation to laboratory facilities. Samples of algae, seagrass and sponges, and mesh bags containing animals from massive corals and turfing algae, were fixed immediately in 5% buffered formalin solution. Live coral samples were placed in sorting trays and flushed three times in fresh water to remove animals, which were transferred to sample containers and fixed in 5% buffered formalin solution. A pilot pair-wise comparison of epifaunal assemblages associated with macroalgae fixed immediately in 5% formalin and washed three times in fresh water showed no significant difference in abundance between the two methods (PERMANOVA, $n = 12$, $t = 0.99$, $P = 0.42$).

Once fixed, epifaunal invertebrates were dislodged from their habitat using a jet of water and by shaking in a bucket, collected on a 125 µm sieve, and stored in 70% ethanol:2% glycerol:28% water solution for up to 12 months before identification and counting. Data were collected to quantify structural characteristics of sampled microhabitats (Table 2.2), and live coral was returned to the reef.

**Table 2.2** Microhabitat structural characteristics. Degree of branching ranges from low (1) to high (9). Massive coral maximum width and length were taken from the entire sampled area; branching was 1. For turfing algae, dead coral and coral rubble maximum width and length were approximate for turf filaments; turf filaments were generally assigned 1 for degree of branching.

| Characteristic | Description | Variable type | Range/levels |
|---|---|---|---|
| **Planar area** | Planar area ($cm^2$) occupied by the sample in the field. | Continuous | 78 – 625 $cm^2$ |
| **Maximum length** | Length (cm) from base to distal tip of sample. | Continuous | 0.2 – 88 cm |
| **Maximum width** | Maximum width (cm) across primary axis of sample. | Continuous | 0.01 – 55 cm |
| **Epiphyte load** | Wet weight (g) of epiphytes growing on sample. | Continuous | 0 – 46 g |
| **Degree of branching** | Complexity metric following (Edgar 1983); analogy derived from stream classification (Horton 1945): order of the primary axis, whenever an axis splits the order increases by one. | Categorical | 1 – 9 |
| **Hardness** | Rigidity and hardness of sample structure | Categorical | 1 – rigid<br>2 – semi-rigid<br>3 – semi-flexible<br>4 – flexible<br><br>See Table S2 for microhabitats allocated to each hardness category |

### 2.4.2 Laboratory processing and data analysis

Invertebrates from each sample were rinsed through a 1 mm sieve and retained animals identified and counted under a dissecting microscope. Identification was performed to family-

level where possible, otherwise to order or phylum (family identification was impractical for < 2% of animals).

Relative abundance data of epifaunal taxa were standardised to abundance per 1 $m^2$ planar area prior to analysis by factoring for the area of sampled microhabitat photographed in the field. Analyses were repeated using abundance by taxa expressed as a proportion of total abundance per sample. Multivariate community analyses of standardised abundance by family data (or higher taxonomic level) were conducted using PRIMER 7, ver. 7.0.13 (Clarke and Gorley 2015). Differences in composition of assemblages associated with different microhabitats were visualised using a canonical discriminant analysis of principal co-ordinates (CAP; (Anderson and Willis 2003)) of $\log_{10}$ (x + 1) transformed data (to account for zero counts and reduce the influence of highly abundant taxa) on a Bray-Curtis resemblance matrix. A permutational analysis of variance (PERMANOVA; (Anderson 2001, McArdle and Anderson 2001, Anderson 2017)) was conducted to test for assemblage differences among microhabitats (fixed effect) and sampling locations (random effect).

Similarity percentages analysis (SIMPER; (Clarke 1993)) of abundance data by order-level taxa revealed 10 taxa contributing most to similarity within microhabitat-associated assemblages (note: caprellid amphipods were grouped separately from other amphipods due to their high abundance at some sites and suspension-feeding habits). Mean percent composition of these taxa for different microhabitats was visualized using R x64 3.6.1 (R Core Team 2019).

Variation in faunal composition was then related to variation in microhabitat structure, based on associations with important physical microhabitat elements. Firstly, a cluster analysis was undertaken on the Bray-Curtis similarity matrix of $\log_{10}$ (x + 1) transformed epifaunal abundance data, individually for each location (Fig. 2.6 (S1)). The maximum number of

clusters defined for each location was arbitrarily set at the number of different microhabitats sampled in that location, and thus varied between locations. The structural characteristics of microhabitat samples (Table 2.2) comprising the samples within each cluster were then averaged, providing a multivariate characterisation of the habitat structure associated with the epifaunal-derived cluster in that location. Principal components analysis (PCA) was then used to visualise separation of clusters from all locations combined, and to relate these to the physical microhabitat structure values (as vectors), and thus identify which structural characteristics consistently contributed to subdivision in the epifaunal community across all locations.

## 2.5 Results

CAP analyses revealed clear groupings of samples among microhabitat categories with very little overlap between fucoid algae and live branching coral microhabitats (Fig. 2.2). Samples taken from fucoid macroalgae, branched and tabular *Acropora*, and turf represented three extremes in assemblage composition, with no microhabitat showing an intermediate community structure between those found on fucoids and *Acropora* coral. Samples from other microhabitats lay intermediate between those from fucoids and turf (grouped as ‘other macrophytes’, Fig. 2.2c), or coral and turf (grouped as ‘sessile invertebrates’, Fig. 2.2c).

Fucoid algae-associated assemblages were dominated by amphipods, whereas live coral assemblages comprised predominantly decapods (Fig. 2.3). Amphipods were a large component of turfing algae-associated assemblages; other macrophytes and sessile invertebrates hosted assemblages with relatively high numbers of polychaetes and molluscs, although amphipods were also important (Fig. 2.3).

Microhabitat and location were both significantly correlated with variation among samples and explained similar levels of total variation (~15%, Table 2.3, Table 2.4). An interaction

between microhabitat and location was also detected, albeit explaining only about half the variation of the factors on their own.

Of the microhabitat structural characteristics considered (Table 2.2), degree of branching and relative hardness explained nearly all variability between groups identified through faunal analysis (the first two components explained 73.1% and 20.8% of total variation, respectively, when based on abundance $m^{-2}$ data, and 71.0% and 22.4% when based on proportional abundance; Fig. 2.4). Interestingly, the variation associated with both these structural characteristics outweighed the variation associated with latitude when compared using PCA (Fig. 2.4). Epifaunal assemblage composition varied considerably with degree of branching; low branching was generally correlated with a higher proportion of polychaetes, high branching with more molluscs, and mid-levels of branching with more amphipods and isopods (Fig. 2.5). The hardest microhabitats tended to support assemblages dominated by decapods, with more polychaetes and then amphipods comprising assemblages associated with increasingly flexible microhabitats. The most flexible microhabitats (i.e. with fine filaments) possessed a relatively even taxonomic composition, with the largest contribution made by amphipods (Fig. 2.5).

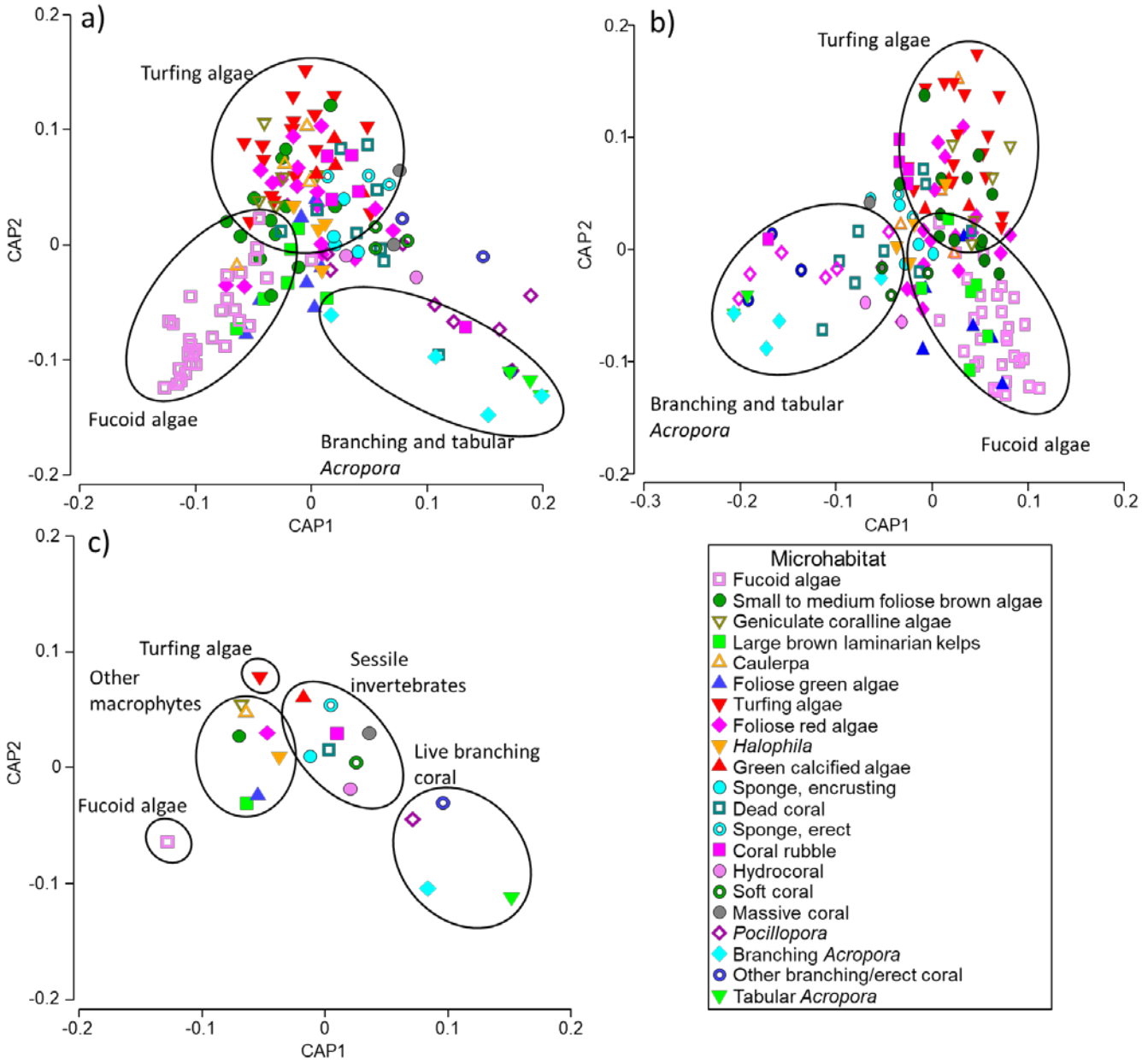



**Fig. 2.2** CAP analyses of samples with microhabitat separation maximised. Taxonomic composition based on **(a)** density of epifaunal taxa (/m$^2$ seabed), and **(b)** abundance of epifaunal taxa as a proportion of total sample abundance. Ellipses in **(a)** and **(b)** group fucoid algae, branching and tabular Acropora, and turfing algae. Mean CAP1 and CAP2 coordinates from **(a)** were used to plot centroids for each microhabitat, shown in **(c)**. Ellipses in **(c)** group microhabitats into fucoid algae, other macrophytes, turfing algae, sessile invertebrates, and live branching coral.

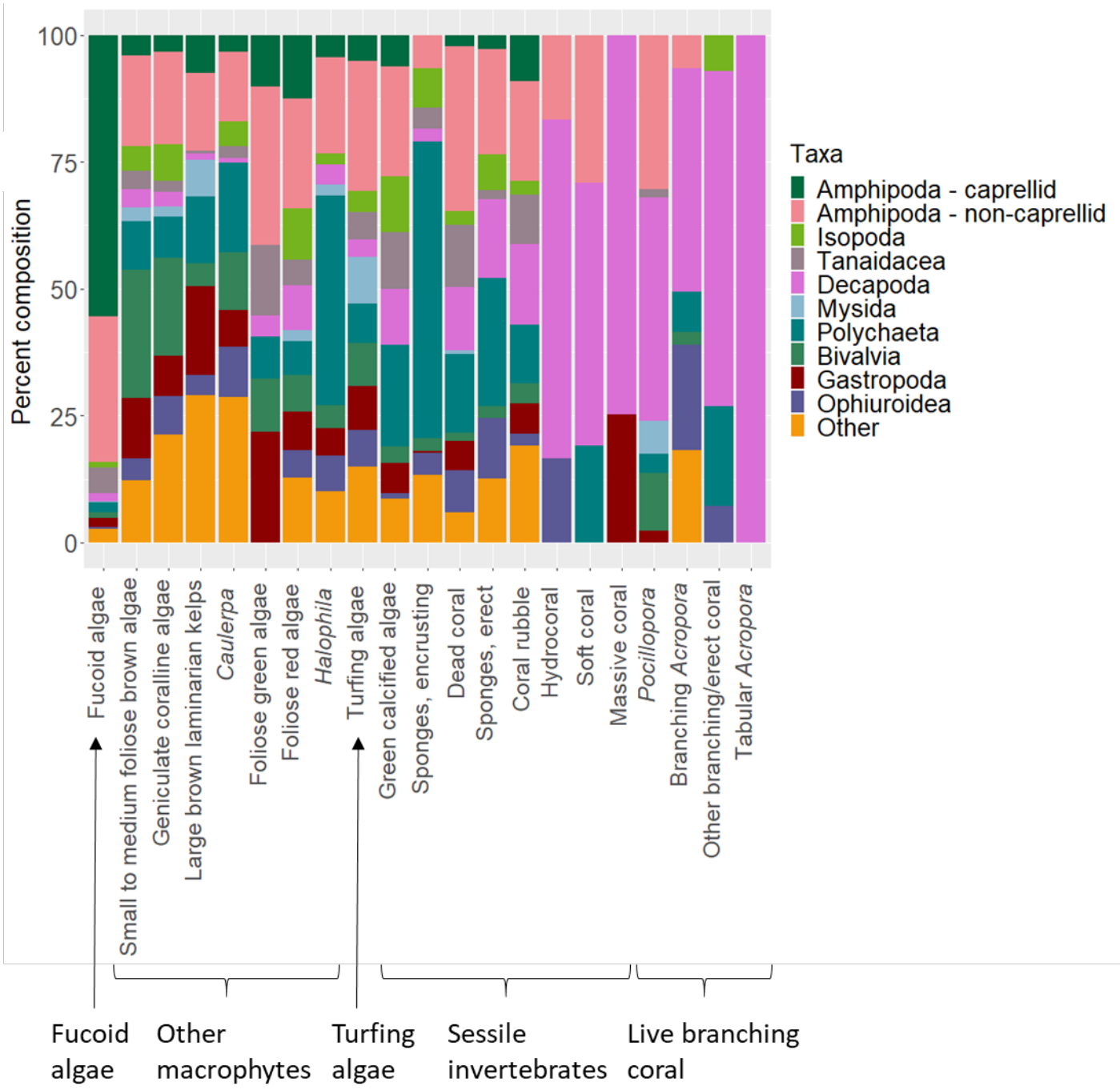



**Fig. 2.3** Percent composition of the ten epifaunal taxa identified by SIMPER analysis as contributing most to similarity within microhabitat-associated assemblages. Microhabitat groups derived from CAP analyses (Fig. 2.2c)). Additional taxa grouped as 'other' comprise: Anthozoa, Asteroidea, Cephalopoda, Chitonida, Clitellata, Crinoidea, Cumacea, Echinoidea, Harpacticoida, Holothuroidea, Insecta, Nemertea, Ostracoda, Platyhelminthes, Pycnogonida, Sabellida, Sagittoidea and Terebellida.

**Table 2.3** Multivariate PERMANOVA assessing effects of microhabitat, location, and their interaction on taxonomic composition, using taxa abundance per $m^2$ planar area, including percentage of variation explained by the different factors.

| **Source** | **Degrees of freedom** | **Sum of squares** | **Mean square** | **Pseudo-*F* ratio** | ***P* value (by permutation)** | **% variation** |
|---|---|---|---|---|---|---|
| **Microhabitat** | 20 | 113580 | 5679 | 2.04 | 0.001 | 14.7 |
| **Location** | 11 | 69758 | 6342 | 2.67 | 0.001 | 13.2 |
| **Microhabitat x Location** | 49 | 136860 | 2793 | 1.17 | 0.018 | 6.8 |
| **Residual** | 71 | 168870 | 2378 | | | 65.3 |
| **Total** | 151 | 555540 | | | | |

**Table 2.4** Multivariate PERMANOVA assessing effects of microhabitat, location, and their interaction on taxonomic composition, using proportion of total abundance per sample, including percentage of variation explained by the different factors.

| **Source** | **Degrees of freedom** | **Sum of squares** | **Mean square** | **Pseudo-*F* ratio** | ***P* value (by permutation)** | **% variation** |
|---|---|---|---|---|---|---|
| **Microhabitat** | 20 | 11870 | 5944 | 1.83 | 0.001 | 14.9 |
| **Location** | 11 | 71590 | 6508 | 2.34 | 0.001 | 12.8 |
| **Microhabitat x Location** | 49 | 159280 | 3251 | 1.18 | 0.008 | 6.7 |
| **Residual** | 70 | 193070 | 2758 | | | 65.4 |
| **Total** | 150 | 601170 | | | | |

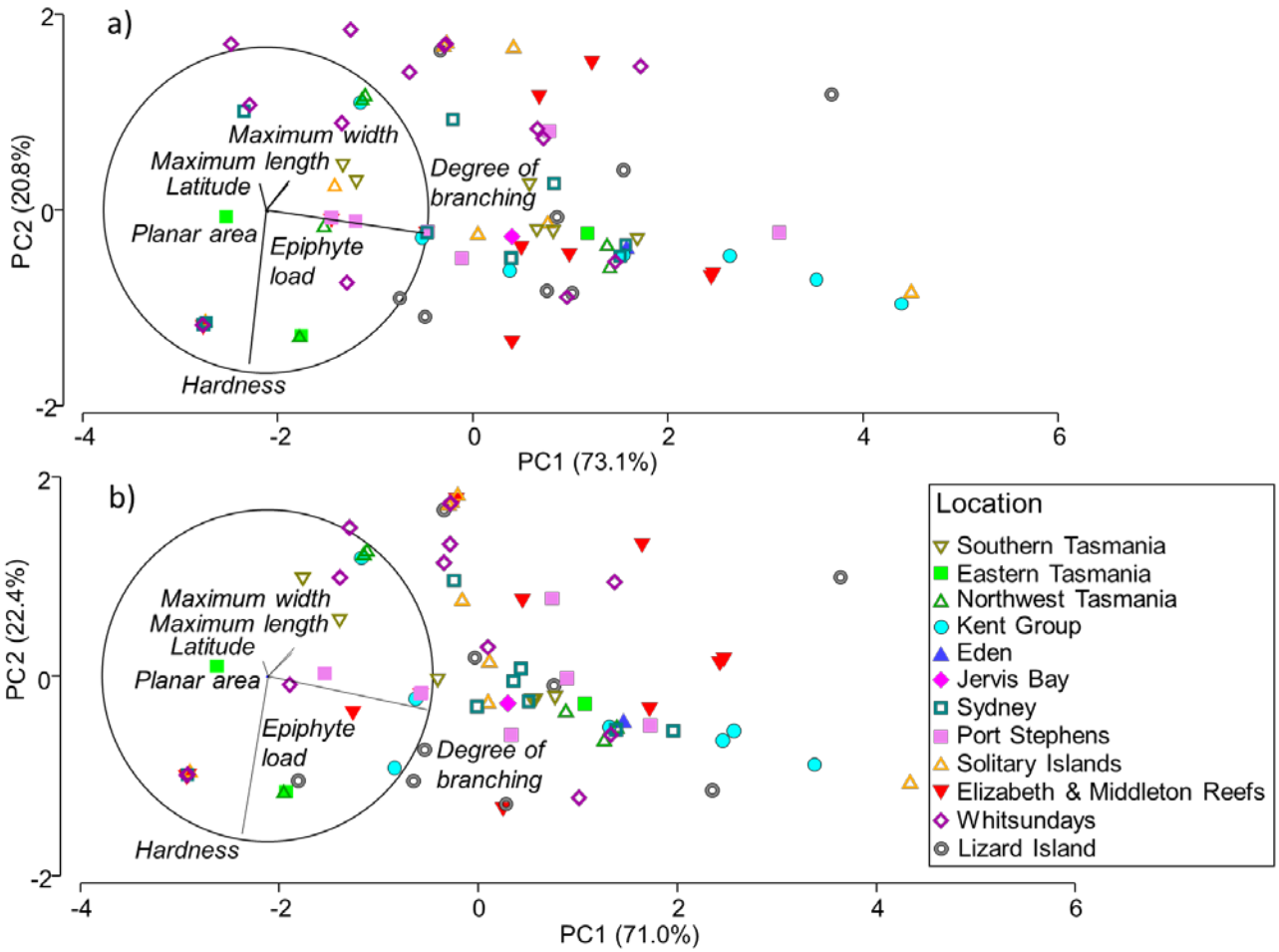



**Fig. 2.4** PCA of the physical structural characteristics of groups identified by clustering samples using epifaunal similarity at each location (abundance by taxa expressed as **(a)** density $m^{-2}$ and **(b)** proportion of total abundance per sample). PC1 closely reflects a branching gradient from low branching (negative PC1 scores; e.g. massive corals, encrusting sponges) to high branching (positive PC1 scores; e.g. foliose red algae). PC2 is highly correlated with hardness of microhabitat, with high hardness (e.g. hard corals) at positive PC2 scores and high flexibility (e.g. turfing algae) at negative PC2 scores. Symbols represent locations from which samples were collected; the PCA does not reflect the latitudinal gradient among locations.

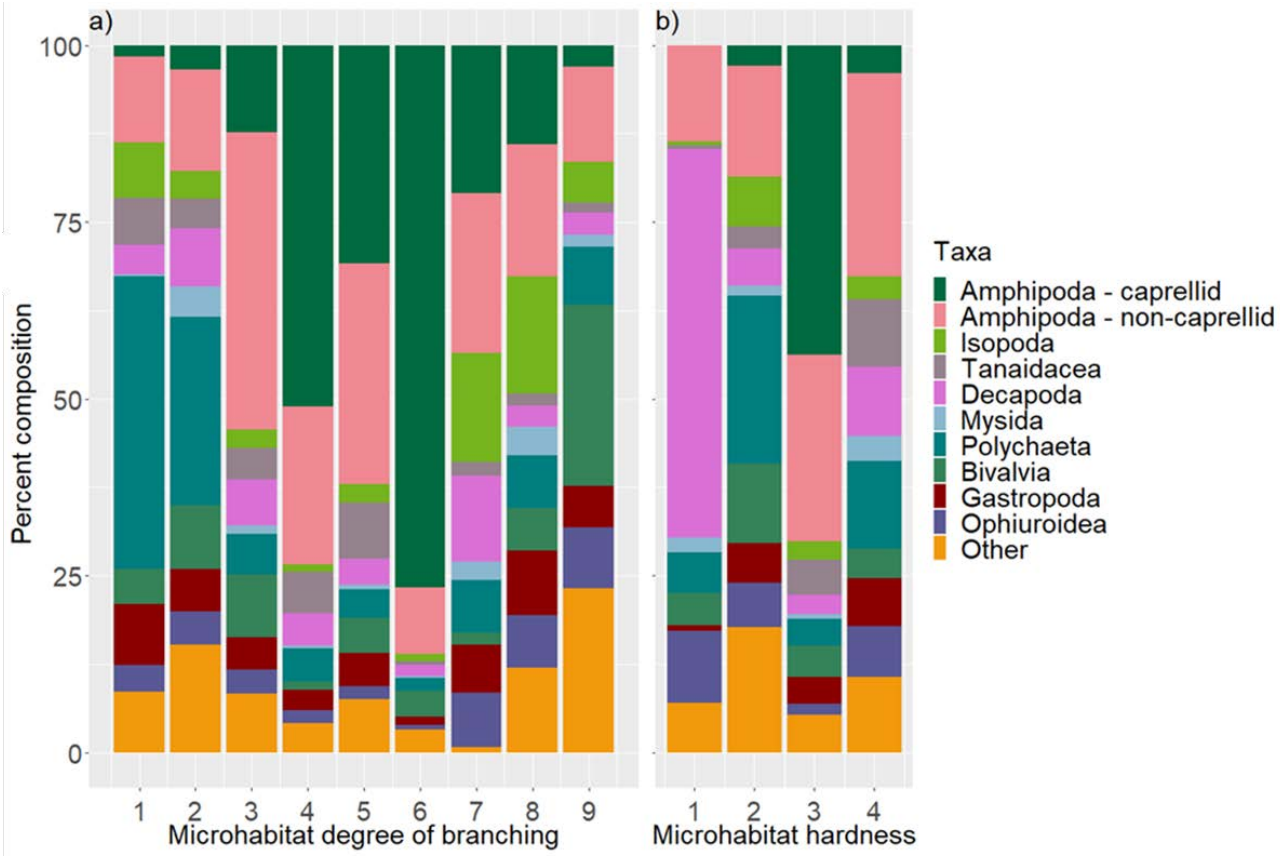



**Fig. 2.5** Percent composition of major taxa at different levels of **(a)** microhabitat degree of branching, and **(b)** relative hardness.

## 2.6 Discussion

### 2.6.1 Habitat structure and epifaunal taxa

Although epifaunal assemblages have been described in relation to distinct benthic microhabitats (Cowles et al. 2009, Kramer et al. 2014), our understanding of the ecology of this group of animals is still poorly developed. Previous studies have found clear associations between epifauna and a number of different coral reef, macroalgal and seagrass microhabitats (Edgar 1992, Stella et al. 2010, Marzinelli et al. 2014), and Kramer et al. (2017) contrasted epifaunal crustacean assemblages in three tropical and three temperate reef microhabitats. To date, no studies have compared epifaunal community structure among more diverse reef microhabitats spanning a temperate to tropical climatic gradient. In the present study of

epifaunal invertebrates associated with 21 microhabitats at locations ranging from temperate macroalgae-dominated reefs to tropical coral reefs, microhabitat was found to strongly affect epifauna. Sampled assemblages partitioned along two gradients that connected turf microhabitats with two other extremes – fucoid macroalgae and live branching coral. Invertebrates associated with erect macrophytes (including seagrasses) grouped between fucoid macroalgae and turf. Epifaunal assemblages associated with rigid, low-profile sessile invertebrate microhabitats (plus green calcareous algae, typically *Halimeda sp.*) fell between live branching coral and turf.

The presence of distinct epifaunal assemblages among microhabitat categories may be explained in part by structural characteristics of the habitats. A wealth of literature describes patterns of taxonomic composition in faunal assemblages associated with structurally diverse habitats (Griffiths et al. 2006, Komyakova et al. 2013, Marzinelli et al. 2014, Torres et al. 2015, Parsons et al. 2016, Lavender et al. 2017). Research investigating epifauna-habitat relations has collectively been undertaken at a diversity of sampling locations, however, most individual studies sampled one location only (Gee and Warwick 1994a, Chemello and Milazzo 2002, Stella et al. 2010, Kramer et al. 2014, Stelling‐Wood et al. 2020). Published studies consistently indicate strong correlations between epifaunal assemblage composition and habitat structure, yet limited research has directly investigated assemblage variation among diverse locations and the interaction between location and habitat structure (but see Kramer et al. (2017)). Despite the PERMANOVA indicating significant differences among locations with regards to the composition of epifaunal assemblages here (Tables 2.3 and 2.4), the PCA indicated that microhabitat structure greatly outweighed influences associated with the broad latitudinal gradient from which samples were collected. Further investigation of epifaunal assemblage metrics such as size structure and overall density and production is needed to better understand the functional implications of these patterns for reef ecosystems.

Habitat complexity is a particularly useful metric that has long been identified as an important factor structuring faunal assemblages (MacArthur and MacArthur 1961, Kovalenko et al. 2012). Degree of branching is a way of quantifying complexity of benthic microhabitats (Edgar 1983), with higher branching equating to more structurally complex habitat (Table 2.2). Degree of branching was the most useful microhabitat characteristic considered here, correlating to a PCA axis that explained 73.1% of variation among clusters of samples after grouping by taxonomic composition at the local scale. Relative hardness was also important, separating microhabitats of differing flexibility (for example, hard corals, semi-rigid macroalgae and flexible filamentous turf). Previous studies have found distinctions in epifaunal crustaceans between hard coral and flexible turf (Kramer et al. 2014), although hardness was not investigated *per se*. In combination, degree of branching and relative hardness explained most of the variation among clusters of samples in our study, suggesting that epifaunal invertebrates depend to a large extent on complexity and flexibility of habitat. These relationships may be mediated by ecological interactions, for example top-down predation pressure (Power 1992, Taylor 1998) or differences in local bottom-up food resources among microhabitats (Hay et al. 1987, Menge 1992).

Previous research highlighting the trophic significance of epifaunal invertebrates suggests that demersal invertivorous fishes and larger invertebrates rely on epifauna as a primary food source (Edgar and Aoki 1993, Taylor 1998, Kramer et al. 2015). Thus, epifaunal habitat selection may reflect predator avoidance and may differ depending on the feeding strategies of local invertivores and their ability to penetrate microhabitats of differing complexity and flexibility. Habitat structural complexity and its interaction with predator-prey relationships has been the subject of ecological discussion for some time (Crowder and Cooper 1982, Grabowski et al. 2008, Warfe et al. 2008). Incorporating community data for fishes and larger mobile invertebrates spatially and temporally associated with epifaunal communities may

clarify mechanisms behind the observed epifauna-habitat relationships, however such intensive co-located sampling across space and time would be highly challenging.

While hard coral heterotrophy largely depends on consumption of zooplankton (Goreau et al. 1971, Houlbréque and Ferrier-Pagés 2009), consumption of epifaunal invertebrates by polyps may influence assemblages associated with these benthic biota. Colonisation of live coral is further complicated by allelopathic and physical defence strategies (e.g. “sweeper tentacles”) utilised by soft and hard corals, respectively, to resist predation and colonisation by epiphytes and epifauna (Coll et al. 1982, Sammarco et al. 1983, Gochfeld 2004).

The observed differences in epifaunal assemblages may also be influenced by bottom-up availability of food resources associated with the different microhabitats. Epifaunal assemblages comprise a diversity of functional groups, including herbivores, detritivores, carnivores and filter-feeders (Newcombe and Taylor 2010, Kramer et al. 2017), and habitat structure may affect the availability of food resources for these different groups. For example, epifaunal herbivores, known as ‘mesograzers’ (Hay et al. 1987), feed on macroalgae as well as microalgae (Kramer et al. 2012) and filamentous turf growing epiphytically on macroalgae, rock, dead coral and coral rubble (Poore et al. 2012). As such, these animals may dominate assemblages associated with more flexible microhabitats, which potentially serve as both shelter and food resources. Other functional groups may respond differently to variation in microhabitat structure as it affects availability of their food resources.

Interestingly, aside from branching and hardness, the other structural characteristics of microhabitats quantified here did not explain much variability in epifaunal assemblages. Previously, larger macroalgal species have been correlated with greater epifaunal abundance and diversity when compared with naturally smaller species (Marzinelli et al. 2014, Torres et al. 2015). Of the microhabitat measures analysed here, maximum length, maximum width

and planar area are functions of the overall size of sampled microhabitat and did not appear to be strong correlates with epifaunal taxonomic composition (i.e. proportional relations between taxa did not change detectably between small and large microhabitats with similar shape). Edgar (1983) related maximum length and width of macroalgae to epifaunal taxonomic composition and, similarly, did not find these microhabitat metrics to be particularly important. Perhaps other faunal metrics, such as abundance and diversity, are better explained by microhabitat size compared to metrics associated with taxonomic composition.

Epiphyte load has been shown to have strong associations with epifauna in macroalgae systems (Edgar 1992, Berthelsen and Taylor 2014). In other research, however, epifaunal response to epiphyte load has been minimal (Edgar 1983) and our results reflect this. The proportion of mesograzers in epifaunal assemblages has been correlated with epiphyte load (Berthelsen and Taylor 2014) and the effect of this microhabitat characteristic may better understood if related to functional rather than taxonomic composition of assemblages.

Nearly all variation (> 90 %) among microhabitat-associated assemblages across sampling locations was explained by degree of branching and relative hardness of microhabitats. Very little unexplained variance remains to be associated with seasonality and other environmental factors that may be hypothesised to be important but that were not assessed in these analyses, such as temperature, wave exposure and turbidity.

### 2.6.2 Macroalgae, coral, and transitions through turf

Benthic habitat transitions to turf-algal dominance have been described as a common element of the degradation process on both coral and macroalgae-dominated reefs (McClanahan et al. 2001, Adjeroud et al. 2009, Barott et al. 2012, Vergés et al. 2014, Wernberg et al. 2016, Reeves et al. 2018). Filamentous turfing algae tend to cover skeletons of bleached corals that

do not recover, and dead branching corals break down over time into turf-covered coral rubble (Nelson et al. 2016, O'Brien and Scheibling 2018). The succession patterns for temperate reefs suffering loss of canopy-forming macroalgal species also tend to show regime shifts towards turf-dominated assemblages (Vergés et al. 2014, Wernberg et al. 2016, Filbee-Dexter and Wernberg 2018, O'Brien and Scheibling 2018), with some cases of extreme herbivory leading to large areas of bare rock or crustose coralline algae cover (Ling 2008). Epifaunal assemblages associated with fucoid macroalgae, turf and branching hard coral also apparently represent three extremes for epifauna community structure, underpinned by structurally distinct microhabitats.

Any major habitat transformation across reef-scapes presents significant challenges for associated fauna. Our results suggest that there is no direct intermediate community for epifauna between associations with macroalgae and live coral; any change in assemblage composition will likely involve a transition through turf-associated epifauna. This reflects previous research (Kramer et al. 2014, Kramer et al. 2017) and the pattern observed in habitat-forming benthic communities, suggesting that epifaunal communities transform consistently with degradation of both macroalgae and live coral habitats via such a transition. Amphipods dominated fucoid algae-associated assemblages, while the majority of epifauna on live branching coral were decapods. Other macrophytes supported relatively high densities of amphipods, molluscs (Gastropoda and Bivalvia) and polychaetes. Other sessile invertebrates (and green calcareous algae) hosted assemblages that predominantly comprised amphipods, polychaetes and decapods. Amphipods were the most abundant taxa in turfing algae assemblages, however turf-associated epifauna showed less dominance of any one taxon than other habitat groups, with more even contributions made by a range of taxonomic orders. On turf-dominated reefs we may expect more even proportional abundance of major epifaunal taxa, without the coral-associated dominance of decapods or macroalgae-associated

dominance of amphipods. Although our results indicate the possibility of consistent epifaunal community transition with changes to benthic habitat, future faunal changes will depend on the existing pool of epifaunal colonisers at each site and site-specific changes to biogenic habitat taxa. Further research partitioning trophic roles, abundance, size structure and productivity of different epifaunal taxa should improve our understanding of the ecological effects brought about by changes to benthic habitat structure on reefs, particularly if the broad environmental gradients associated with latitude and climatic zone are directly incorporated.

### 2.6.3 Conclusions

A diversity of environmental and anthropogenic factors are combining to significantly alter the structure of reef benthos globally, typically from highly complex three-dimensional coral or kelp habitat to low-profile habitat dominated by turfing algae (Vergés et al. 2014, Filbee-Dexter and Wernberg 2018, Ling et al. 2018b). Such changes will directly affect epifaunal invertebrate communities living in close association with surfaces. This is particularly important for reef food webs, given the crucial role small mobile epifaunal invertebrates play in linking local primary production to higher trophic levels (Taylor 1998, Newcombe and Taylor 2010). With loss of corals and macroalgae – or shifts between the two (Hughes et al. 2007) – large changes in the relative abundance of available prey taxa for invertivores are to be expected. Inconsistencies in trophic effects of such habitat transformation may be expected across broad biogeographic scales, reflecting variation in local invertivore communities and other trophic groups. Incorporating fish and larger invertebrate community data into spatial models with epifauna may further refine understanding of habitat transformation effects on reef food webs. By understanding how epifauna relate to different benthic microhabitats, much more accurate predictions can be made of the full range of consequences of reef degradation to subtidal ecosystems.

## 2.7 Acknowledgements

This study was supported by Australian Research Council grants to GJE and SDL, and an Australian Postgraduate Award to KMF. Fieldwork was additionally supported by the Marine Biodiversity Hub – a collaborative partnership supported through the Australian Government's National Environmental Science Programme, as well as Parks Australia, the Sydney Institute for Marine Science, and the Australian Museum's Lizard Island Research Station.

## 2.8 Supplementary material

**Table 2.5 (S1)** Sampling information for each microhabitat shows locations at which collection occurred, and number of samples per location.

Note: air-lifted microhabitats refer to those habitats requiring collection with venturi-powered vacuum with a 500 µm mesh collection bag secured over the outlet. *Number of samples = 1 sample per microhabitat per site; data averaged if more than one sample collected per site.

| Microhabitat category | Location | Number of samples* |
|---|---|---|
| Large brown laminarian kelps | Southern Tas | 1 |
| | Northwest Tas | 1 |
| | Kent Group | 1 |
| | Sydney | 2 |
| | Port Stephens | 1 |
| Fucoid algae | Southern Tas | 8 |
| | Eastern Tas | 3 |
| | Northwest Tas | 1 |
| | Kent Group | 2 |
| | Eden | 2 |
| | Jervis Bay | 3 |
| | Sydney | 6 |
| | Port Stephens | 2 |
| | Solitary Islands | 1 |
| | Lizard Island | 1 |
| Small to medium foliose brown algae | Southern Tas | 1 |

| | | |
|---|---|---|
| | Northwest Tas | 2 |
| | Kent Group | 2 |
| | Sydney | 3 |
| | Port Stephens | 1 |
| | Solitary Islands | 1 |
| | Whitsundays | 1 |
| | Lizard Island | 3 |
| Caulerpa | Kent Group | 1 |
| | Northwest Tas | 1 |
| | Whitsundays | 1 |
| | Elizabeth & Middleton Reefs | 1 |
| Green calcified algae | Elizabeth & Middleton Reefs | 2 |
| | Lizard Island | 2 |
| Foliose green algae | Southern Tas | 3 |
| | Eastern Tas | 1 |
| | Elizabeth & Middleton Reefs | 2 |
| Foliose red algae | Southern Tas | 2 |
| | Kent Group | 3 |
| | Sydney | 2 |
| | Port Stephens | 1 |
| | Solitary Islands | 2 |
| | Elizabeth & Middleton Reefs | 2 |
| | Whitsundays | 3 |
| | Lizard Island | 2 |
| Geniculate coralline algae | Kent Group | 1 |
| | Northwest Tas | 1 |
| | Sydney | 2 |
| | Port Stephens | 1 |
| Turfing algae | Eastern Tas | 1 |
| | Northwest Tas | 2 |
| | Kent Group | 2 |
| | Sydney | 1 |
| | Port Stephens | 1 |
| | Solitary Islands | 1 |
| | Elizabeth & Middleton Reefs | 2 |
| | Whitsundays | 2 |
| | Lizard Island | 3 |
| *Halophila* | Sydney | 2 |
| | Port Stephens | 2 |
| Sponges, encrusting | Southern Tas | 1 |
| | Sydney | 1 |
| | Solitary Islands | 1 |
| | Whitsundays | 1 |

| | | |
|---|---|---|
| Sponges, erect | Southern Tas | 1 |
| | Elizabeth & Middleton Reefs | 1 |
| | Whitsundays | 1 |
| | Lizard Island | 1 |
| Hydrocoral | Whitsundays | 2 |
| Soft coral | Elizabeth & Middleton Reefs | 2 |
| | Whitsundays | 5 |
| | Lizard Island | 2 |
| *Pocillopora* | Solitary Islands | 2 |
| | Elizabeth & Middleton Reefs | 2 |
| | Whitsundays | 2 |
| | Lizard Island | 3 |
| Branching *Acropora* | Solitary Islands | 2 |
| | Elizabeth & Middleton Reefs | 3 |
| | Whitsundays | 1 |
| Tabular *Acropora* | Elizabeth & Middleton Reefs | 3 |
| Massive coral | Lizard Island | 1 |
| | Whitsundays | 2 |
| Other branching/erect coral | Elizabeth & Middleton Reefs | 5 |
| | Whitsundays | 1 |
| | Lizard Island | 2 |
| Dead coral | Solitary Islands | 1 |
| | Elizabeth & Middleton Reefs | 3 |
| | Whitsundays | 2 |
| | Lizard Island | 3 |
| Coral rubble | Elizabeth & Middleton Reefs | 2 |
| | Lizard Island | 3 |

**Table 2.6 (S2)** Microhabitats and categories of relative hardness.

| **Hardness category** | **Microhabitats** |
|---|---|
| **1 – rigid** | Hydrocoral |
| | Massive coral |
| | *Pocillopora* |
| | Branching *Acropora* |
| | Other branching/erect coral |
| | Tabular *Acropora* |
| **2 – semi-rigid** | Geniculate coralline algae |
| | Large brown laminarian kelps |
| | Green calcified algae |
| | Sponges, encrusting |
| | Sponges, erect |

| | |
|---|---|
| | Soft coral |
| **3 – semi-flexible** | Fucoid algae<br>Small to medium foliose brown algae<br>Caulerpa<br>Foliose green algae<br>Foliose red algae<br>*Halophila* |
| **4 - flexible** | Turfing algae<br>Dead coral<br>Coral rubble |

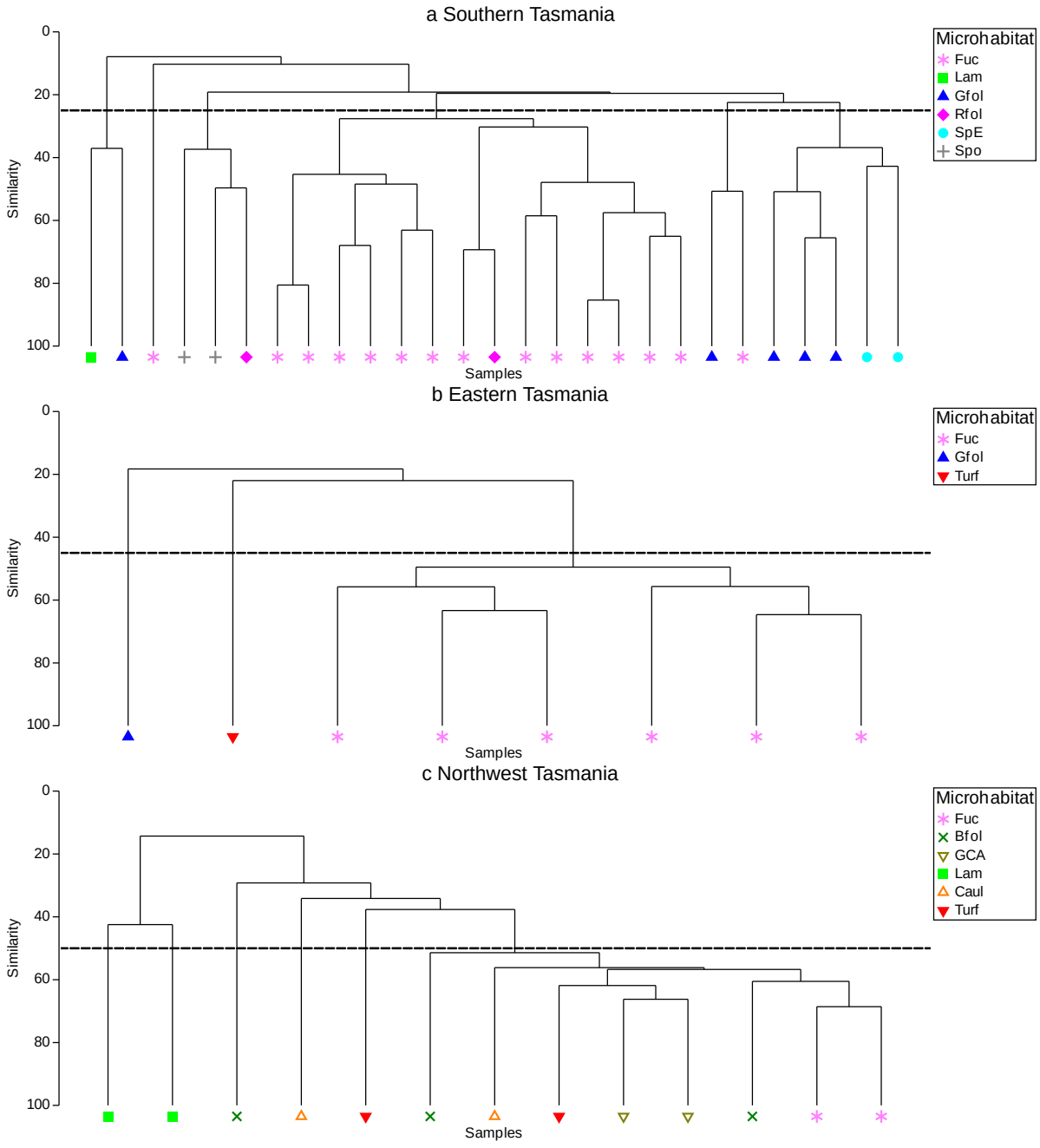
**Table 2.7 (S3)** Results of SIMPER analysis showing taxa (by Order level identification) most important for similarity among samples within each microhabitat type.

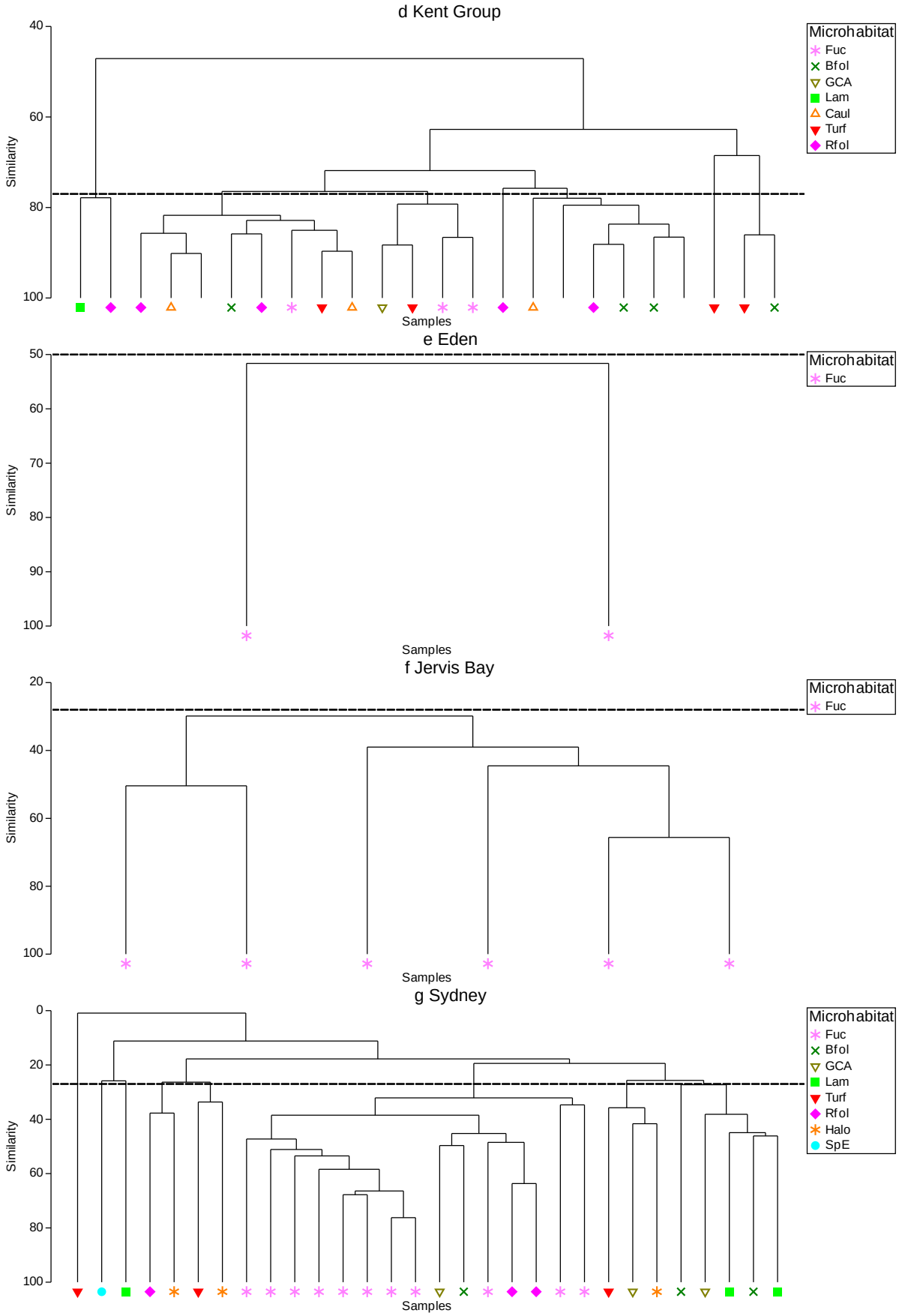
| Taxa | Average abundance | Average similarity | Sim/SD | Contribution (%) | Cumulative (%) |
|---|---|---|---|---|---|
| **Large brown laminarian kelps** | | | | | |
| **Amphipoda (non-caprellid)** | 2.54 | 16.03 | 3.95 | 41.44 | 41.44 |
| **Gastropoda** | 2.48 | 11.30 | 1.16 | 29.23 | 70.67 |
| **Fucoid algae** | | | | | |
| **Amphipoda (non-caprellid)** | 4.96 | 13.61 | 3.57 | 25.58 | 25.58 |
| **Polychaeta** | 3.05 | 7.85 | 1.74 | 14.74 | 40.32 |
| **Amphipoda (caprellid)** | 3.98 | 7.61 | 1.26 | 14.29 | 54.61 |
| **Gastropoda** | 2.79 | 6.61 | 1.52 | 12.42 | 67.03 |
| **Decapoda** | 2.42 | 4.77 | 0.99 | 8.97 | 76.00 |
| **Small to medium foliose brown algae** | | | | | |
| **Gastropoda** | 3.68 | 11.94 | 2.99 | 25.83 | 25.83 |
| **Amphipoda (non-caprellid)** | 3.69 | 10.52 | 1.90 | 22.76 | 48.59 |
| **Polychaeta** | 2.57 | 5.31 | 0.84 | 11.48 | 60.08 |
| **Bivalvia** | 2.44 | 4.23 | 0.82 | 9.14 | 69.22 |
| **Decapoda** | 1.90 | 3.73 | 0.67 | 8.07 | 77.29 |
| **Caulerpa** | | | | | |
| **Amphipoda (non-caprellid)** | 3.50 | 10.90 | 2.15 | 35.43 | 35.43 |

| | | | | | |
|---|---|---|---|---|---|
| **Gastropoda** | 2.44 | 4.22 | 0.79 | 13.71 | 49.14 |
| **Polychaeta** | 2.88 | 3.84 | 0.90 | 12.49 | 61.63 |
| **Bivalvia** | 2.63 | 3.58 | 0.91 | 11.63 | 73.26 |
| **Green calcified algae** | | | | | |
| **Amphipoda (non-caprellid)** | 3.45 | 14.08 | 3.60 | 31.57 | 31.57 |
| **Gastropoda** | 2.09 | 7.73 | 0.91 | 17.34 | 48.91 |
| **Polychaeta** | 2.77 | 7.62 | 0.90 | 17.08 | 65.99 |
| **Isopoda** | 2.42 | 7.17 | 0.90 | 16.08 | 82.07 |
| **Foliose green algae** | | | | | |
| **Amphipoda (non-caprellid)** | 3.04 | 25.27 | 1.26 | 70.07 | 70.07 |
| **Foliose red algae** | | | | | |
| **Amphipoda (non-caprellid)** | 3.61 | 10.92 | 1.22 | 27.70 | 27.70 |
| **Gastropoda** | 2.51 | 5.74 | 0.97 | 14.57 | 42.27 |
| **Decapoda** | 2.31 | 4.90 | 0.61 | 12.44 | 54.70 |
| **Polychaeta** | 2.23 | 4.49 | 0.71 | 11.38 | 66.09 |
| **Amphipoda (caprellid)** | 2.32 | 3.77 | 0.74 | 9.58 | 75.66 |
| **Geniculate coralline algae** | | | | | |
| **Amphipoda (non-caprellid)** | 4.43 | 10.46 | 3.79 | 19.87 | 19.87 |
| **Gastropoda** | 3.74 | 9.53 | 3.62 | 18.10 | 37.97 |
| **Bivalvia** | 3.69 | 8.17 | 3.28 | 15.52 | 53.49 |
| **Amphipoda (caprellid)** | 2.59 | 4.47 | 0.99 | 8.50 | 61.99 |
| **Polychaeta** | 2.97 | 4.42 | 1.14 | 8.41 | 70.41 |
| **Turfing algae** | | | | | |
| **Amphipoda (non-caprellid)** | 3.22 | 8.31 | 1.81 | 18.50 | 18.50 |
| **Gastropoda** | 2.68 | 7.52 | 1.37 | 16.75 | 35.25 |
| **Polychaeta** | 2.40 | 6.57 | 1.71 | 14.62 | 49.87 |
| **Tanaidacea** | 1.96 | 4.04 | 0.77 | 9.01 | 58.88 |
| **Bivalvia** | 2.22 | 3.99 | 1.11 | 8.89 | 67.76 |
| **Decapoda** | 1.59 | 3.81 | 0.93 | 8.47 | 76.24 |
| ***Halophila*** | | | | | |

| | | | | | |
|---|---|---|---|---|---|
| **Amphipoda (non-caprellid)** | 3.17 | 15.41 | 9.96 | 30.11 | 30.11 |
| **Polychaeta** | 3.27 | 11.87 | 2.69 | 23.19 | 53.29 |
| **Ophiuroidea** | 1.93 | 6.96 | 0.90 | 13.59 | 66.89 |
| **Decapoda** | 1.54 | 4.84 | 0.91 | 9.44 | 76.33 |
| **Sponges, encrusting** | | | | | |
| **Polychaeta** | 5.31 | 21.91 | 5.55 | 36.45 | 36.45 |
| **Isopoda** | 3.48 | 13.78 | 2.53 | 22.94 | 59.39 |
| **Amphipoda (non-caprellid)** | 3.37 | 13.50 | 4.19 | 22.46 | 81.85 |
| **Sponges, erect** | | | | | |
| **Ophiuroidea** | 3.57 | 18.44 | 1.92 | 42.81 | 42.81 |
| **Isopoda** | 2.92 | 12.73 | 2.55 | 29.55 | 72.37 |
| **Hydrocoral** | | | | | |
| **All similarities are zero** | | | | | |
| **Soft coral** | | | | | |
| **Decapoda** | 3.10 | 48.95 | 3.06 | 80.48 | 80.48 |
| ***Pocillopora*** | | | | | |
| **Decapoda** | 2.78 | 28.02 | 0.99 | 91.71 | 91.71 |
| **Branching *Acropora*** | | | | | |
| **Decapoda** | 3.43 | 20.45 | 0.86 | 73.88 | 73.88 |
| **Tabular *Acropora*** | | | | | |
| **Decapoda** | 4.21 | 83.64 | 9.68 | 100.00 | 100.00 |
| **Massive coral** | | | | | |
| **Decapoda** | 1.62 | 70.84 | SD = 0 | 100.00 | 100.00 |
| **Other branching/erect coral** | | | | | |
| **Decapoda** | 3.40 | 47.17 | 3.19 | 100.00 | 100.00 |
| **Dead coral** | | | | | |
| **Amphipoda (non-caprellid)** | 3.75 | 11.72 | 1.65 | 27.78 | 27.78 |
| **Decapoda** | 3.37 | 11.18 | 1.45 | 26.48 | 54.27 |
| **Tanaidacea** | 2.60 | 6.24 | 1.00 | 14.79 | 69.06 |
| **Polychaeta** | 2.45 | 4.44 | 0.76 | 10.53 | 79.59 |
| **Coral rubble** | | | | | |
| **Amphipoda (non-caprellid)** | 3.48 | 15.37 | 3.72 | 35.11 | 35.11 |
| **Decapoda** | 2.72 | 10.93 | 1.06 | 24.96 | 60.07 |
| **Polychaeta** | 2.15 | 4.03 | 0.60 | 9.20 | 69.27 |

| | | | | | |
|---|---|---|---|---|---|
| **Amphipoda (caprellid)** | 1.79 | 3.55 | 0.57 | 8.11 | 77.38 |

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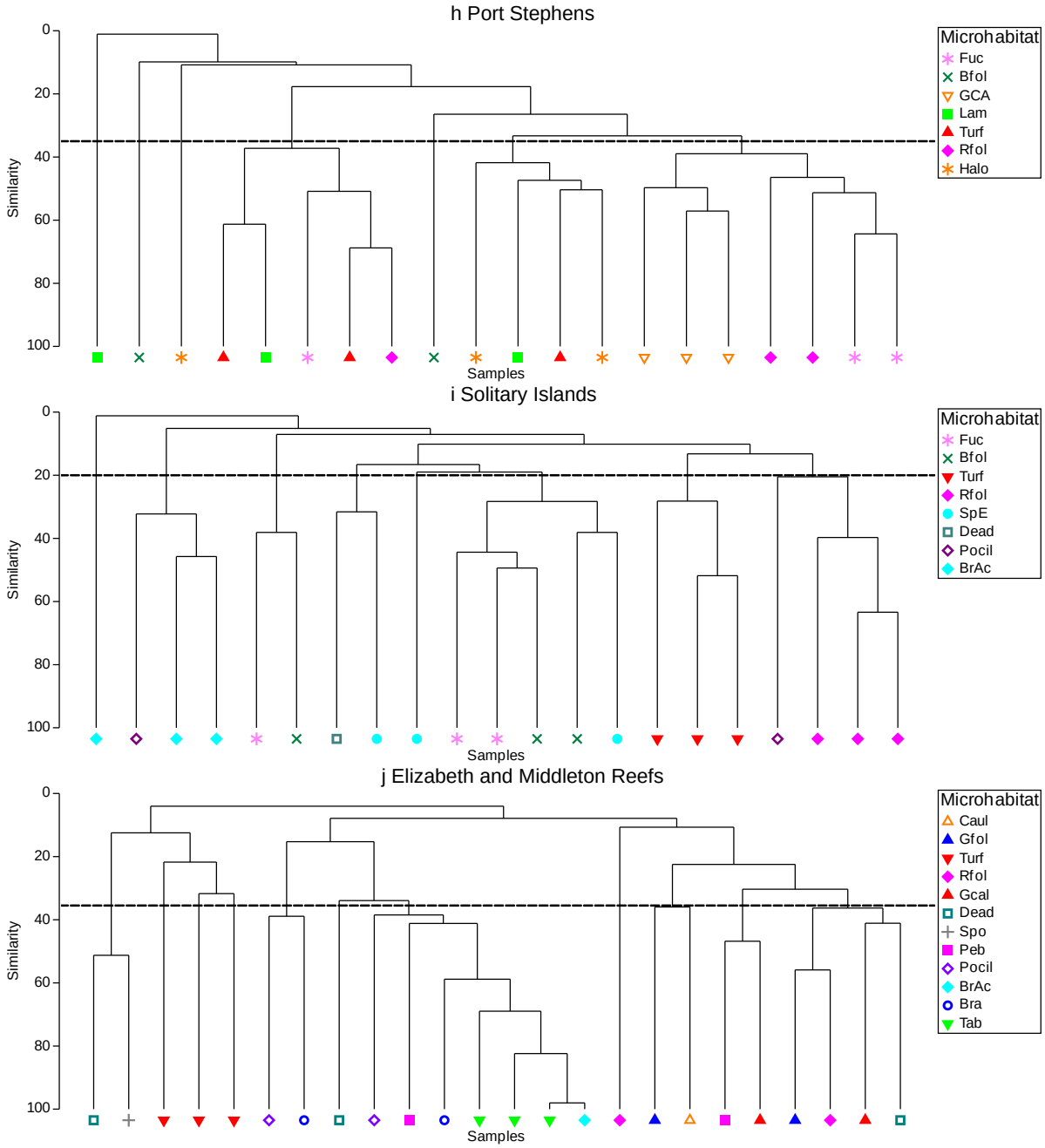
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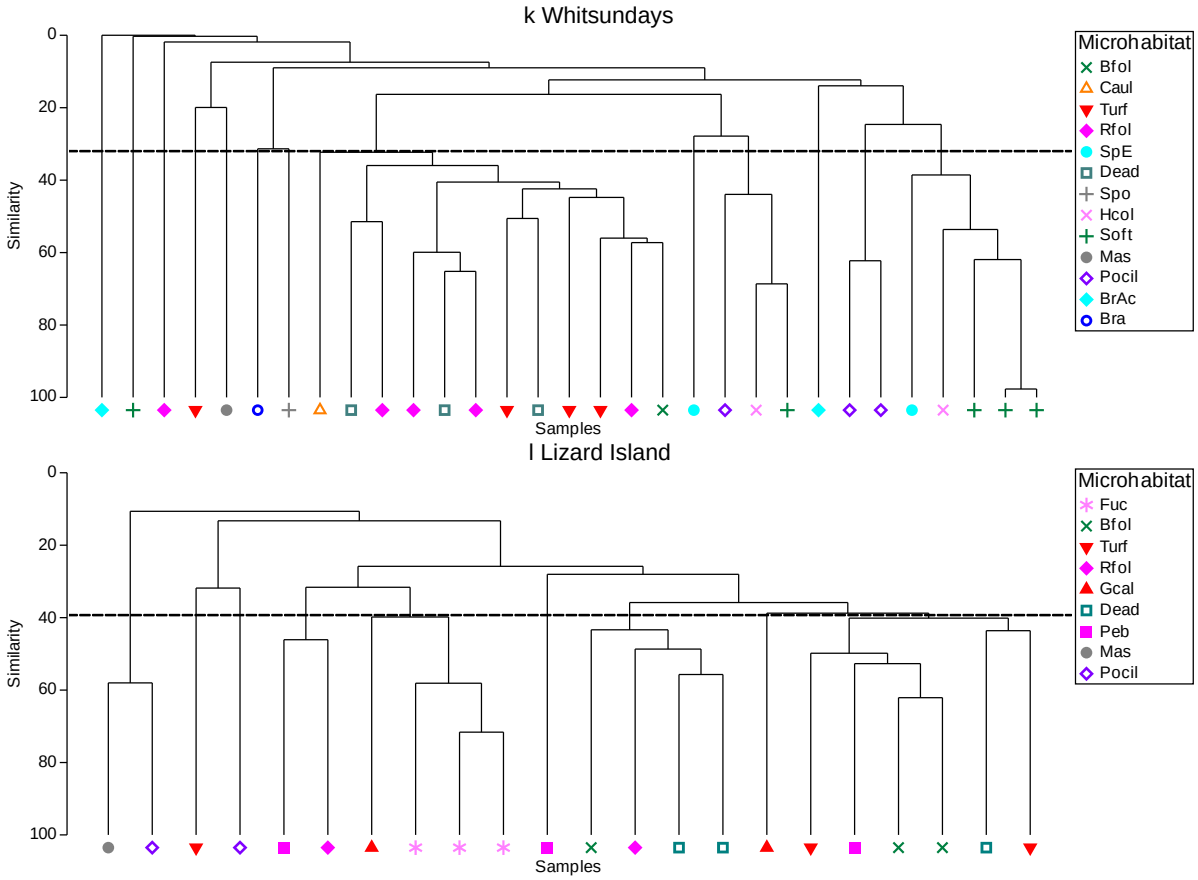


**Fig. 2.6 (S1)** Dendrograms of cluster analyses undertaken on the Bray-Curtis Similarity matrix of $\log_{10}$ (x + 1) transformed epifaunal abundance $m^{-2}$ data, individually for each location: **(a)** Southern Tasmania, **(b)** Eastern Tasmania, **(c)** Northwest Tasmania, **(d)** Kent Group, **(e)** Eden, **(f)** Jervis Bay, **(g)** Sydney, **(h)** Port Stephens, **(i)** Solitary Islands, **(j)** Elizabeth and Middleton Reefs, **(k)** Whitsundays, **(l)** Lizard Island. Dotted line indicates similarity level at which clusters were selected for each location.

# Chapter 3

# SMALL INVERTEBRATE CONSUMERS PRODUCE CONSISTENT SIZE SPECTRA ACROSS REEF HABITATS AND CLIMATIC ZONES

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**Preface:**

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Fraser KM, Stuart-Smith RD, Ling SD, Edgar GJ (2020) Small invertebrate consumers produce consistent size spectra across reef habitats and climatic zones. Oikos. DOI: 10.1111/oik.07652

In Chapter 3 I compare the size structure of epifaunal assemblages across habitats and sampling locations. I estimate site-scale size spectra using microhabitat distribution data and I compare size spectra among four distinct groups of microhabitats between temperate and tropical reefs. Chapter 3 builds on the variation in epifauna among microhabitats identified in Chapter 2, using the complete size-range of animals and grouping microhabitats based loosely on the microhabitat extremes identified in Chapter 2. Chapter 3 links to Chapter 4 by providing a model of size spectra analysis and highlighting distinctions between live coral and turfing algae habitats. Chapter 3 links to Chapter 5 by showing how varying size spectra can contribute to assemblage productivity.

## 3.1 Abstract

Changes in invertebrate body size-distributions that follow loss of habitat-forming species can potentially affect a range of ecological processes, including predation and competition. In the marine environment, small crustaceans and other mobile invertebrates ('epifauna') represent a basal component in reef food webs, with a pivotal secondary production role that is strongly influenced by their body size-distribution. Ongoing degradation of reef habitats that affect invertebrate size-distributions, particularly transformation of coral and kelp habitat to algal turf, may thus fundamentally affect secondary production. Here we explored variation in size spectra of shallow epifaunal assemblages (i.e. the slope and intercept of the linear relationship between log abundance and body size at the assemblage level) across 21 reef microhabitats distributed along an extensive eastern Australian climatic gradient from the tropical northern Great Barrier Reef to cool temperate Tasmania. When aggregated across microhabitats at the site scale, invertebrate body size spectra (0.125 to 8 mm range) were consistently log-linear ($R^2$ ranging 0.87 to 0.98). Size spectra differed between, but not within, major groups of microhabitats, and exhibited little variability between tropical and temperate biomes. Nevertheless, size spectra showed significant tropical/temperate differences in slopes for epifauna sampled on macroalgal habitats, and in elevation for soft coral and sponge habitats. Our results reveal epifaunal size spectra to be a highly predictable macro-ecological feature. Given that variation in epifaunal size spectra among groups of microhabitats was greater than variation between tropical and temperate biomes, we postulate that ocean warming will not greatly alter epifaunal size spectra directly. However, transformation of tropical coral and temperate macroalgal habitats to algal turfs due to warming will alter reef food web dynamics through redistribution of the size of prey available to fishes.

## 3.2 Keywords

macrofauna, macroalgae, coral reef, epifauna, meiofauna, food web

## 3.3 Introduction

Global climate change and local anthropogenic pressures are driving collapse of natural habitats within many ecosystems. Examples include direct impacts of clear-felling on forests (Nepstad et al. 1999), effects of climate-altered fire regimes on forests (Enright et al. 2015) and savannas (Scheiter et al. 2015), and coastal modifications to wetlands (Mitsch and Hernandez 2013). Widespread loss of key biogenic habitats in reef systems – such as corals (Hughes et al. 2018, Stuart-Smith et al. 2018) and kelp forests – is occurring due to direct (Krumhansl et al. 2016, Vergés et al. 2016, Wernberg et al. 2016) and indirect impacts of ocean warming (Ling 2008, Bates et al. 2017), and exacerbated by anthropogenic activity such as dredging (Lenihan and Peterson 2004), trawling (Kaiser et al. 2002), and eutrophication and pollution from land-based run-off (Bell 1992, Wolff et al. 2018). While habitat transformation is readily observable, understanding the ecological consequences requires knowledge on how food webs are altered by changes in habitat, particularly for taxa that are strongly linked to particular habitat types. Shifts in body size-distributions of important prey taxa can be an important mechanism of ecological change, as animal size-distribution affects prey availability to different predators (Ling et al. 2009, Kramer et al. 2015).

Small mobile epifaunal invertebrates (‘epifauna’) play a pivotal role in shallow food webs by trophically linking primary producers to higher carnivores (Edgar and Shaw 1995, Newcombe and Taylor 2010, Kramer et al. 2013). Impacts of widespread habitat change on epifauna, as well as any direct effects of climate change, will thus affect higher trophic levels

including fishery resources (Connolly 1994, Edgar 1999), which are more directly valued by society. However, little information exists on how basal food web dynamics vary among reef habitat states or in different climate regimes (Edgar 1993, Kramer et al. 2017). Consequently, the extent that phase-shifts among reef habitats and changing ocean climates affect the basal epifaunal trophic level, and thus the availability of food resources to higher trophic levels, remains speculative.

Epifaunal taxonomic composition varies with the structure of habitats (Stella et al. 2010, Marzinelli et al. 2014), and habitat structure can overshadow the influence of environmental variation on the composition of epifaunal taxa along a broad latitudinal gradient (Fraser et al. 2020a) (Chapter 2). This suggests that on any given patch of reef, changing habitats may have greater impacts on food availability for invertivores than changing temperatures. Significant differences in the composition, biomass and production of epifaunal crustacean assemblages were recently identified between a temperate and a tropical location, on habitats of similar structure (Kramer et al. 2017), suggesting potential for complex interactive effects between habitat and temperature. However, availability of epifaunal invertebrates as prey for invertivores is influenced by more than taxonomic composition.

Benthic invertivores show strong size-specific prey selection (Edgar and Aoki 1993, Kramer et al. 2015), hence knowledge of body size distributions within epifaunal assemblages is critical for understanding the availability of food resources for different invertivore species. When the frequency distribution of individual body sizes is plotted for a given trophic group (often using a linear model – referred to as the size spectrum (White et al. 2007, Edwards et al. 2017)), the abundance of animals typically declines with increasing body size (Peters and Wassenberg 1983, Marquet et al. 1990, Damuth 1991). Hence, size spectra are generally negatively sloped, and the steepness of the slope indicates variation in the relative contributions of larger versus smaller animals (Trebilco et al. 2015). Size spectra slopes tend

to be consistent in undisturbed aquatic systems (Sheldon et al. 1972, Trebilco et al. 2013), with inconsistencies observed when predator abundance is overestimated or when energy subsidies are provided from non-local sources (Trebilco et al. 2013). Explanations of variation in size spectra slopes are generally based on a few ecological principles, for example size-selective predation pressure from outside the modelled community, whereby larger body-sizes are generally more readily consumed, leading to steeper size spectra (Rassoulzadegan and Sheldon 1986). Steeper size spectra may also be related to inefficiencies in the transfer of energy from prey to predators within the modelled community (Lindeman 1942, Trebilco et al. 2013). Variation in the primary production and ecological state of the system may also affect community size spectra, for example the slopes of plankton size spectra in freshwater lakes were found to decrease from oligotrophic to eutrophic conditions (Sprules and Munawar 1986).

To date, no published studies have investigated the size spectrum of epifaunal assemblages on structurally diverse habitats among multiple locations extending from tropical to temperate reefs. A recent study comparing biomass size spectra of infaunal communities across a latitudinal gradient of 60-81°N found no significant latitudinal variation (Mazurkiewicz et al. 2020). However, other related ecological attributes clearly vary with latitude (Poulin and Hamilton 1995, Fisher et al. 2010), including the abundance and diversity of potential epifaunal predators (Ebeling and Hixon 1991, Edgar et al. 2017). The trophic state of reef systems also tends to differ substantially with latitude; low latitude coral reefs are typically oligotrophic systems (McClanahan et al. 2002a), while high-latitude macro-algae dominated rocky reefs are typically more eutrophic (Burkepile and Hay 2006). Given these latitudinal trends, and the strong compositional differences in epifauna driven by habitat structure (Fraser et al. 2020a) (Chapter 2), the epifaunal size spectrum could potentially vary between tropical and temperate ecosystems and with habitat structure.

Here we investigate variation in the abundance size spectrum of epifaunal assemblages at 11 diverse shallow reef locations in eastern Australia. This region is a known hotspot of ocean warming (Poloczanska et al. 2007, Babcock et al. 2019), with climate-driven habitat transformations observed to extend from the Great Barrier Reef (Stuart-Smith et al. 2018) to subtropical coral reefs (Kim et al. 2019) to warm-temperate reefs off south-eastern mainland Australia (Marzinelli et al. 2014) and cool-temperate rocky reefs off Tasmania (Johnson et al. 2011, Wernberg et al. 2011). Specifically, we test the hypothesis that epifaunal abundance size spectra will vary as a result of interactive effects between habitat type and climate zone (i.e. tropical vs. temperate). Our overarching goals is to shed light on the likely consequences of ongoing warming and habitat transformation on this basal component of reef ecosystems.

## 3.4 Materials and methods

### 3.4.1 Study area and field sampling

Shallow reefs were sampled at 11 locations along the eastern seaboard of Australia, from southern Tasmania (43.3°S) to Lizard Island in the northern Great Barrier Reef (14.7°S) (Fig. 3.1). Sampling locations spanned a mean annual temperature gradient of 14.3–27.1°C. A total of 148 samples of benthic microhabitats (Tables 3.1 and 3.3) and associated epifauna were collected in September and October 2015, and over a 22 month period from January 2017 to November 2018. At each location, between 2 and 11 sites were sampled with numbers of sites and samples depending on logistic constraints and the timing of each sampling trip. Sites were separated by a minimum distance of 2.5 km.

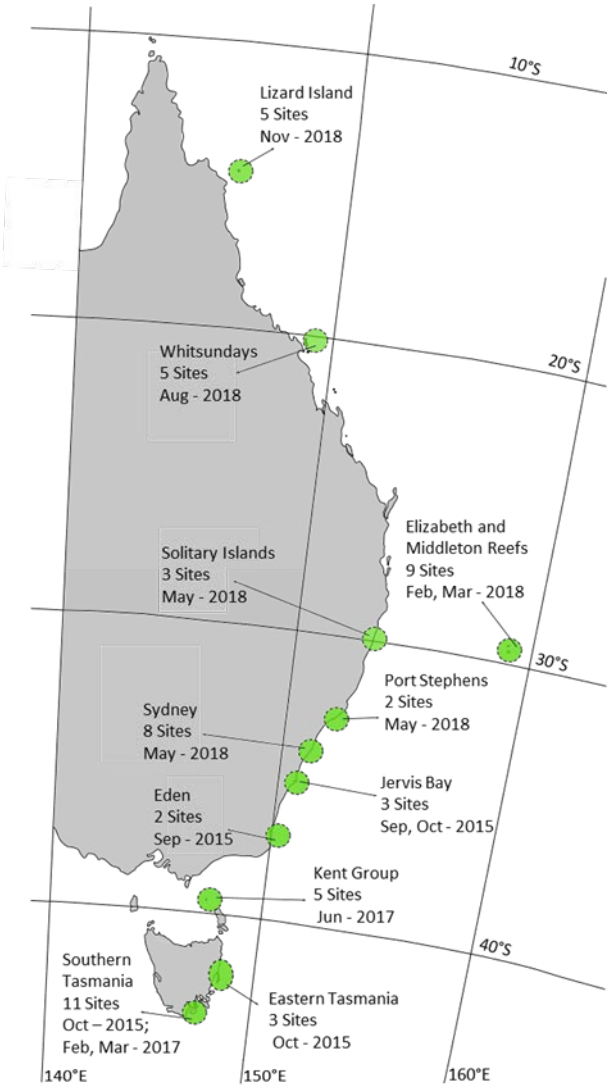



**Fig. 3.1** Map of sampling locations showing sampling dates and number of sites.

Site sampling involved SCUBA-based collection of a subset of 20 different microhabitat types concurrently with associated epifaunal invertebrates. The distinction between microhabitats was based on a combination of taxonomy and morphology, as applied in previous studies to classify seabed habitat types (Cresswell et al. 2017) and by the CATAMI scheme (Althaus et al. 2015), which provides a national standard for Australian benthic habitat classification. Microhabitats were selected for sampling as they were sighted, with a minimum distance of 5 m between selected samples. The presence of different microhabitats

at each site determined which were collected, with efforts made to sample one replicate of each microhabitat available at each site. Each microhabitat was identified as belonging to one of four major habitat groups based on taxonomy and morphology (Table 3.1).

Following Fraser et al. (2020a) (Chapter 2), prior to collection, a 25 cm x 25 cm grid-subdivided quadrat was placed over the selected microhabitat and photographed to quantify the seabed area covered by the microhabitat. Macroalgae, sponges and soft corals were removed with a sharp knife; branching hard corals were removed with a chisel and rubber mallet; coral rubble was collected by hand. Samples were immediately enclosed and sealed within plastic bags. Epifauna associated with turfing algae and massive corals, which could not easily be removed for sampling, were collected using a venturi-powered vacuum with a 500 µm mesh bag secured over the outlet. The entire planar area within the quadrat was swept in suction samples. The mesh bag was removed immediately after sampling and sealed in a plastic bag. The venturi suction method resulted in loss of meiofaunal animals (<0.5 mm body size) through the mesh bag.

Samples of microhabitats and associated epifauna were taken to the surface and preserved in the field. All samples, except those of live corals, were fixed immediately in 5 % buffered formalin solution. Live coral samples were rinsed 3 times in fresh water to remove animals, which were then fixed in 5 % buffered formalin solution. A previous study showed no significant differences in abundance of epifauna removed from microhabitats fixed immediately in 5 % formalin compared with those rinsed 3 times in fresh water (Fraser et al. 2020a).

Samples were transported to laboratory facilities and, once fixed, epifauna were removed from their habitat using a jet of fresh water and by shaking in a bucket. Epifauna were

collected on a 125 µm sieve and stored in 70 % ethanol:2 % glycerol:28 % water solution for up to 12 months before processing.

**Table 3.1** Microhabitats sampled, with habitat group, description and example genera.

| **Microhabitat category** | **Habitat group** | **Description** | **Example genera** |
|---|---|---|---|
| Fucoid algae | Macroalgae | Robust, vertical, complex-branching brown algae, leafy appearance | *Sargassum, Xiphophora, Acrocarpia, Cystophora* |
| Large brown laminarian kelps | Macroalgae | Large habitat forming, overstorey kelp, wide lamina | *Ecklonia, Lessonia* |
| Small to medium foliose brown algae | Macroalgae | Sheet-like, soft plate-like, or filamentous brown understorey algae | *Zonaria, Dictyota, Padina, Lobophora, Halopteris* |
| *Caulerpa* | Macroalgae | Green algae of genus *Caulerpa*, thick vertical growth (often finely branching) from horizontal stolon | *Caulerpa* |
| Foliose green algae | Macroalgae | Thin sheet-like, thick branching, or filamentous green algae, vertical growth habit | *Ulva, Codium, Chlorodesmis, Chaetomorpha* |
| Foliose red algae | Macroalgae | Flexible red algae, branched or leafy, vertical growth habit | *Plocamium, Gracilaria, Pterocladia, Acathophora, Laurencia* |
| Geniculate coralline algae | Macroalgae | Red calcified algae, fine branches jointed or segmented, vertical growth habit | *Corallina, Amphiroa* |

| | | | |
|---|---|---|---|
| Green calcified algae | Macroalgae | Green algae, branching into calcified segments, vertical growth habit | *Halimeda* |
| Turfing algae | Turfing algae | Fine filamentous turfing algae ≤ 2 cm high growing densely or matted on hard substrate, with minimal sandy sediment entrapped | *Feldmannia, Polysiphonia* |
| Dead coral | Turfing algae | Dead erect coral skeleton overgrown with fine filamentous turfing algae | *Acropora (dead), Pocillopora (dead)* |
| Coral rubble | Turfing algae | Broken dead coral rubble overgrown with fine filamentous turfing algae | *Acropora (dead), Pocillopora (dead), Porites (dead)* |
| Soft coral | Sessile invertebrates | Semi-erect, lobed soft corals | *Lobophytum, Sarcophyton, Xenia* |
| Sponges, encrusting | Sessile invertebrates | Sponges forming a crust over substrate | *Mycale, Aplysilla, Tedania, Chondrilla* |
| Sponges, erect | Sessile invertebrates | Erect sponges rising from substrate, colony height greater than width, appears solid in cross-section | *Halichondria, Echinoclathria, Ancorina* |
| Hydrocoral | Live coral | Branching or foliaceous erect colonies | *Millepora* |
| Massive coral | Live coral | Slow-growing, massive, small polyp stony corals | *Porites* |
| *Pocillopora* | Live coral | Stony corals forming branched colonies, genus *Pocillopora* | *Pocillopora* |
| Branching *Acropora* | Live coral | Stony, branching corals forming colonies, genus *Acropora* | *Acropora* |
| Tabular *Acropora* | Live coral | Stony branching corals forming tabular colonies | *Acropora* |

| | | | |
|---|---|---|---|
| Other branching/erect coral | Live coral | Fine or robust branching, columnar or foliaceous stony coral colonies | *Porites*, *Turbinaria*, *Seriatopora*, *Stylophora* |

Concurrent with sample collection, 20 random photographs of substrata and benthic organisms were taken along a 50 m survey transect through the site. Photographs ('photo-quadrats') were taken directly downwards from approximately 50 cm above the seabed to encompass an area of approximately 30 cm x 30 cm. Photo-quadrats were not available for sites sampled in 2015 (see Fig. 3.1); consequently, photo-quadrats taken from the same sites in the nearest year of surveys (2013) were used to characterise the habitat composition at these sites.

Tropical and temperate biomes divided locations north or south of 30°S, depending on whether reef was dominated by macroalgae (temperate) or coral (tropical) (Malcolm et al. 2010). The Solitary Islands (approximately 30°S) are situated in a tropical-temperate biotone (Malcolm et al. 2010), supporting rocky reef with a combination of macroalgae and a veneer of attached corals (Dalton and Roff 2013). Preliminary analysis indicated that this location grouped with the other temperate locations in non-metric multidimensional scaling (MDS) analysis of the taxonomic composition of sampled assemblages (Fig. 3.5 (S1); Table 3.7 (S1)), so was classified as temperate.

Structural characteristics of sampled microhabitats (Table 3.2) were assessed, based on characteristics identified by Edgar (1994) and Fraser et al. (2020a) (Chapter 2) as important for epifaunal community structure. Variation in structural characteristics among habitat groups and biomes was visualised using box plots in R x64 3.6.1 (R Core Team 2019) using the *tidyverse* package (Wickam et al. 2019).

**Table 3.2** Microhabitat structural characteristics. Degree of branching ranges from low (1) to high (9). Massive coral maximum height was taken from the entire sampled area; branching was 1. For turfing algae, dead coral and coral rubble maximum height were approximated for turf filaments; turf filaments were generally assigned 1 for degree of branching; degree of branching for dead coral and coral rubble was based on the structure of the coral skeleton.

| Characteristic | Description | Range/levels |
|---|---|---|
| **Maximum height** | Height (cm) from base to distal tip of sample. | 0.2 – 88 cm |
| **Degree of branching** | Complexity metric following (Edgar 1983); analogy derived from stream classification (Horton 1945): order of the primary axis, whenever an axis splits the order increases by one. | 1 – 9 |
| **Flexibility** | Flexibility of microhabitat structure. | 1 – rigid<br>2 – semi-rigid<br>3 – semi-flexible<br>4 – flexible |

### 3.4.2 Laboratory processing

Invertebrates from each sample were washed of formalin and passed through a nested series of 12 sieves stacked in descending order of mesh size, following a $\log_{\sqrt{2}}$ series (8, 5.6, 4.0, 2.8, 2.0, 1.4, 1.0, 0.71, 0.5, 0.355, 0.25, 0.18, 0.125 mm, after Edgar (1990b)). Invertebrates retained on each sieve were washed into petri dishes, identified and counted under a dissecting microscope, with data binned by sieve mesh size. Identification was performed to order level where possible, otherwise to phylum (<2% of animals).

### 3.4.3 Data analysis

For each sample collected using the venturi suction method, abundance estimates of smaller animals (< 0.5 mm) were extrapolated by taking the slope and intercept of the linear regression ($\log_{10}$ (abundance + 1) against $\log_{10}$ (sieve mesh size)) for mesh sizes 0.5–2 mm.

This extrapolation seemed reasonable given extremely high linearity in abundance/body size relationships for habitats sampled to 0.125 mm sieve body size (see Results). The linear regression slope and intercept were used to estimate $\log_{10}$(abundance + 1) for each of the sieves with mesh size <0.5 mm; data were then back-transformed.

Because strong relationships exist between epifaunal biomass and light irradiance (Edgar, 1993), which is a planar metric in relation to the seabed, epifaunal abundance data by size bin were standardised to 1 $m^2$ seabed area (Fraser et al. 2020a) (Chapter 2). Standardisation by seabed area also allowed comparison of epifaunal size spectra data to densities of other trophic groups (e.g. primary producers, benthic invertebrates, fishes), which are typically expressed per square metre of seabed. Moreover, alternative ways of standardising microhabitats generate bias towards species that respond to that particular feature; for example, in the study of 109 common macrofaunal species by Edgar et al. (1983), only 20, 13, 10, and 8 species were significantly associated with epiphyte dry weight, wet algal weight, algal surface area, and dry algal weight, respectively.

Data analyses tested variation in epifaunal size spectra in association with microhabitats and habitat groups, and locations and biomes distributed along the latitudinal gradient (Table 3.3). We found no effect of temperature within biome on size spectra slopes for different microhabitats (ANCOVA; $F = 3.57_{1,50}, 2.9_{1,48}$; $p = 0.06, 0.08$; for tropical and temperate biomes respectively); consequently, subsequent analyses focused on tropical/temperate comparisons only.

**Table 3.3** Factors tested according to their influence on variation in the size spectra of epifaunal assemblages. Nested factors are indicted by parentheses enclosing the factor in which they are nested.

| Factor | Fixed/Random | Number of levels |
|---|---|---|
| Habitat group | Fixed | 4 |
| Microhabitat (Habitat group) | Random | 20 |
| Biome | Fixed | 2 |
| Location (Biome) | Random | 11 |

#### *3.4.3.1 Accounting for habitat variation among sampling locations*

The fraction of cover provided by microhabitats was estimated using data derived from photo-quadrat analysis. At each site, size distribution estimates for all microhabitats were summed to give an estimate of site-level epifaunal density per size bin. Photo-quadrats were assessed to estimate the fraction of cover provided by each microhabitat within a site. Within each site, 95% of the cover of living benthic microhabitats was represented by microhabitats from Table 3.1.

For each site, the proportional cover of each microhabitat was multiplied by the density of epifauna in each size bin from a sample of the same microhabitat collected from that site. When a microhabitat was recorded in photo-quadrat data but not collected at a given site, epifaunal size distribution data from another site within the same location were used. Microhabitats in photo-quadrat data for which no epifaunal data existed comprised <5% of cover at any site and were omitted from analyses. We assume that this data interpolation would add little error to site estimates because variation between microhabitats within major habitat types at different locations (i.e., microhabitat x location interaction, see Results) was low.

The relationship between epifaunal density and size at the site-level was estimated using linear regression in R x64 3.6.1 (R Core Team 2019) using the *tidyverse* package (Wickam et al. 2019) (Edwards et al. 2017), as:

$$\ln(density) \sim \ln(size)$$

where size is the midpoint of each size bin. The slope of this linear relation was the response of interest (the size spectrum slope). Zeros were treated as missing values as those values were likely to be closer to 0.1 than 0 with further sampling. Variation in slopes between biomes and among locations (nested within biome) was examined using univariate permutational analysis of variance (PERMANOVA; (Anderson 2001, McArdle and Anderson 2001, Anderson 2017)).

#### *3.4.3.2 Assessing the interactive effects of habitat, location, and biome on size spectra*

Variation in sample-level size spectra slopes among microhabitats, habitat groups, locations and biomes was examined using univariate permutational analysis of variance (PERMANOVA; (Anderson 2001, McArdle and Anderson 2001, Anderson 2017)). The size spectrum slope for each sample was calculated using a linear regression (ln(density) against ln(mid-point of each size bin)) in R (R Core Team 2019) (Edwards et al. 2017), with zeros treated as missing values. The original tested model included covariates: habitat group, microhabitat (nested within habitat group), biome, and location (nested within biome), and all interaction terms. Following Winer et al. (1991), terms for which $P>0.25$ were removed from the second tested model, which included: habitat group, microhabitat (habitat group), biome, habitat group x biome, microhabitat (habitat group) x location (biome).

Mean epifaunal size spectra slopes were subsequently estimated for each combination of biome and habitat group. Calculations of size spectra for turf and massive coral microhabitats

excluded size bins <0.5 mm as loss of smaller animals due to suction sampling meant data were inaccurate.

Variation in the density contribution of different taxonomic groups across size spectra, among habitat groups, and between biomes was visualised using R (R Core Team 2019). Most invertebrates (93 %) were crustaceans, so epifauna were subdivided into three taxonomic groups: Decapoda, Peracarida and Harpacticoida, with additional taxa comprising a fourth group 'other invertebrates'. Decapods dominated the largest size bins, peracarids the intermediate, and harpacticoids the smallest. Size bins were combined into five groups to more clearly visualize patterns of variation: 0.125–0.18, 0.25–0.355, 0.5–0.71, 1–1.4, 2–2.8, and 4–8 mm.

## 3.5 Results

### *3.5.1* Size spectra variation among sampling locations

Using site-level estimates of epifaunal density per size bin (i.e., aggregated across the microhabitats observed at each site), neither slopes nor intercepts differed significantly between tropical and temperate biomes (Table 3.4). Variation in slopes among locations (nested within biome) was, however, significant (Table 3.4). In order to visualise the differences between locations, the slopes of location-level plots of size spectra, which were compiled using the mean epifaunal density in each size bin across sites within locations, were highly linear with extremely good fits ($R^2$ >0.8; Fig. 3.2). A slight deviation from this log-linear pattern was observed in southern Tasmania, however a relatively high $R^2$ value (0.81) justified plotting these data using a linear model for ease of comparison with other locations.

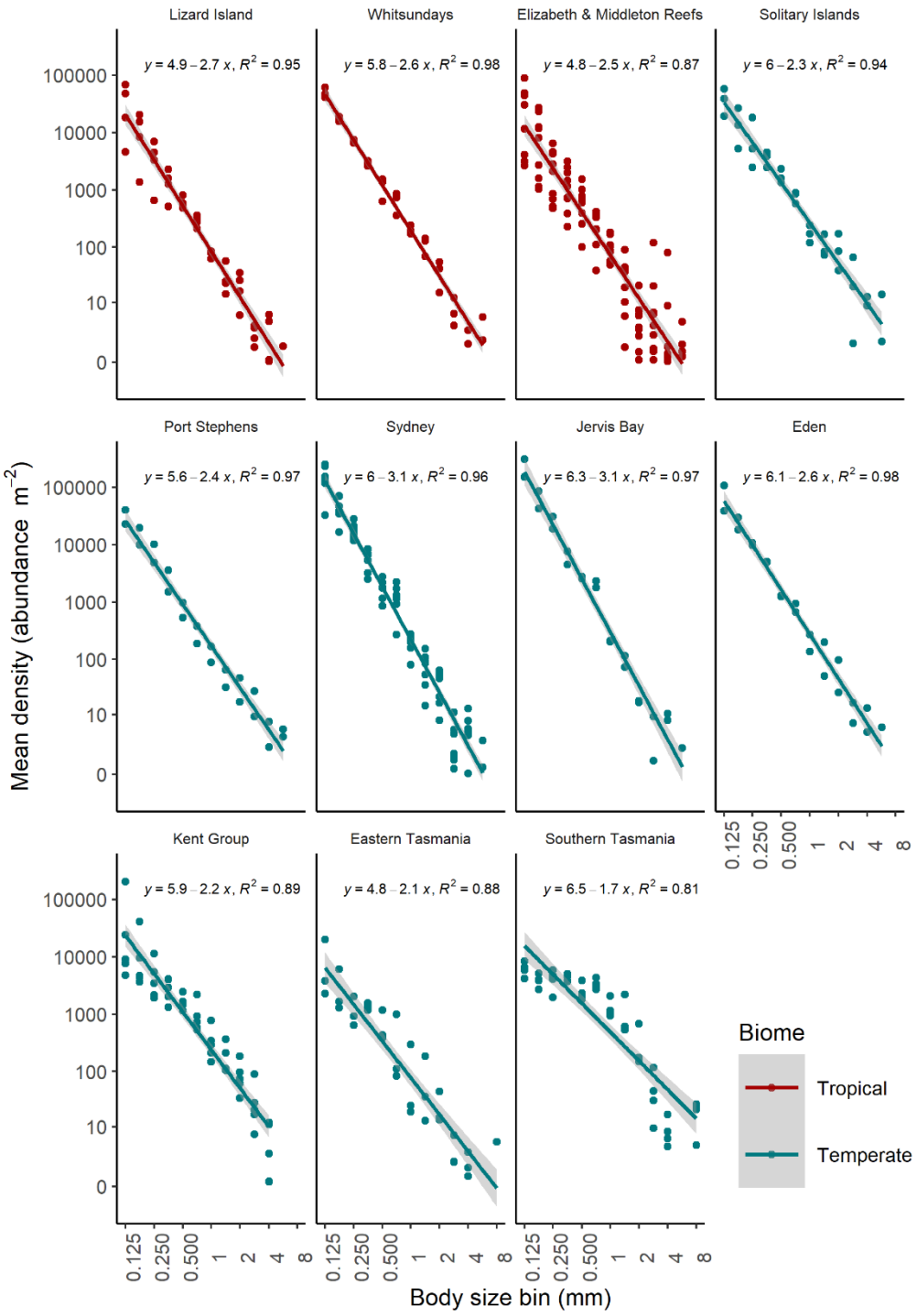



**Fig. 3.2** Size spectra relating mean density (ln(density) against ln(size bin mid-point)) of epifauna for each sampling location, estimated by summing proportional cover of benthic microhabitats at each site. Locations are arranged left to right from lowest to highest latitude. Points represent density estimates within a size bin for individual sites; grey shading represents 95% confidence intervals. Y-axis breaks are presented on a $\log_{10}$ scale rather than $\log_e$ scale for ease of interpretation.

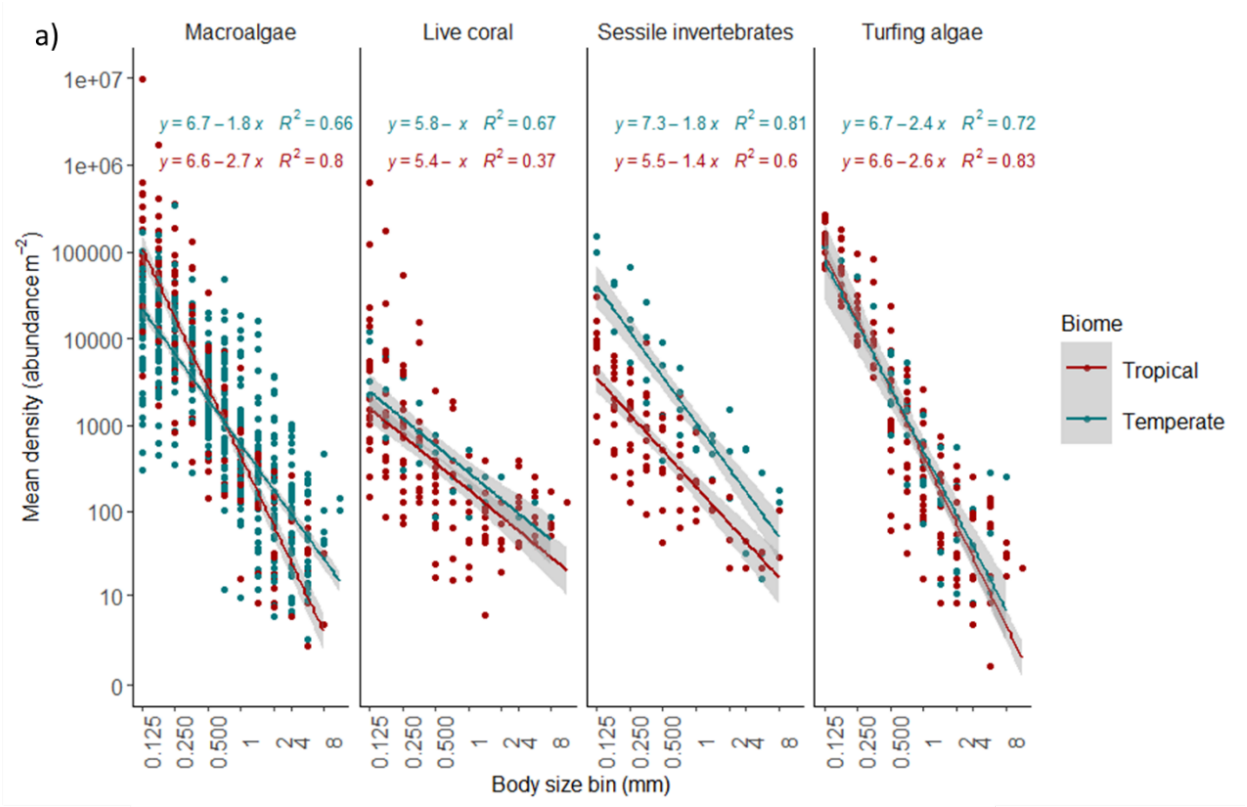
**Table 3.4** Univariate PERMANOVA assessing effects of biome (tropical or temperate) and location (nested within biome) on the slope and intercept of site-level epifaunal size spectra. Nested factors are indicted by parentheses enclosing the factor in which they are nested. Effects highlighted in bold were significant at alpha <0.05. Negative values for percentage of variation explained by each factor are recorded as 0.

| Source of variation | Degrees of freedom | Mean square | Pseudo-*F* ratio | *P* value (by permutation) | % variation |
|---|---|---|---|---|---|
| Size spectrum slope | | | | | |
| Biome | 1 | 0.32 | 0.40 | 0.577 | 0 |
| **Location (Biome)** | **9** | **0.78** | **5.67** | **0.001** | **53.2** |
| Residual | 33 | 0.14 | | | 46.8 |
| Total | 43 | | | | |
| Size spectrum intercept | | | | | |
| Biome | 1 | 5.46 | 5.35 | 0.053 | 36.1 |
| **Location (Biome)** | **9** | **0.99** | **3.50** | **0.011** | **25.9** |
| Residual | 33 | 0.28 | | | 38.0 |
| Total | 43 | | | | |

### 3.5.2 Interactions between habitat, location, and biome

No significant variation in size spectra slopes was evident between microhabitats within habitat groups (Table 3.5), but slopes differed among the broader habitat groups (Table 3.6). Size spectra slopes were linear with a good fit ($R^2$ = 0.60-0.83) for all combinations of habitat group and biome, except for tropical live coral ($R^2$ = 0.37) (Fig. 3.3a). PERMANOVA indicated a significant interaction between habitat group and biome (Table 3.6), suggesting tropical-temperate variation in size spectra slopes differed between habitat groups. Variation in structural characteristics among habitat groups and between biomes was assessed to help clarify possible reasons for temperate and tropical size spectra differing for some habitat types (Fig. 3.3b, c, d). Notably, components of variation for all assessed factors were less

than for residual error, indicating that none of the assessed factors greatly affected slope relative to unaccounted variability.


a)
Macroalgae
Live coral
Sessile invertebrates
Turfing algae
y = 6.7 – 1.8 x R² = 0.66
y = 6.6 – 2.7 x R² = 0.8
y = 5.8 – x R² = 0.67
y = 5.4 – x R² = 0.37
y = 7.3 – 1.8 x R² = 0.81
y = 5.5 – 1.4 x R² = 0.6
y = 6.7 – 2.4 x R² = 0.72
y = 6.6 – 2.6 x R² = 0.83
Mean density (abundance m⁻²)
1e+07
1e+06
100000
10000
1000
100
10
0
0.125
0.250
0.500
1
2
4
8
Body size bin (mm)
Biome
Tropical
Temperate

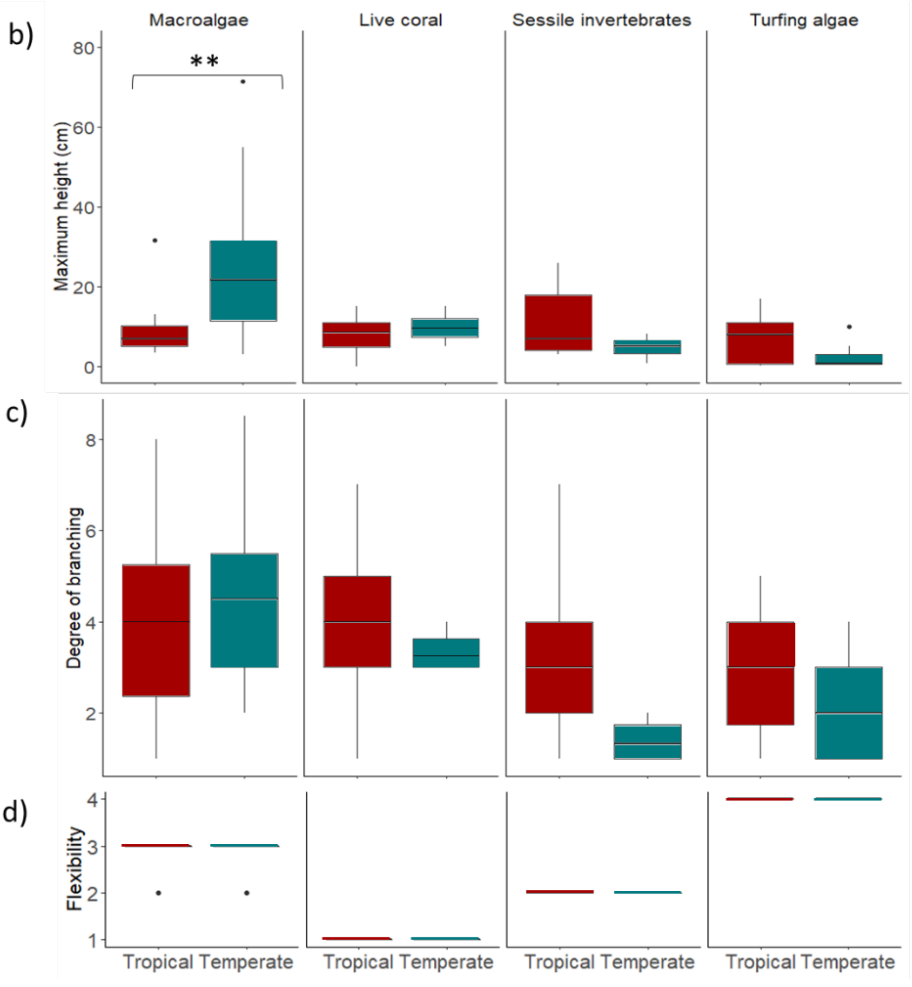

b)
Macroalgae
Live coral
Sessile invertebrates
Turfing algae
**
Maximum height (cm)
80
60
40
20
0
c)
Degree of branching
8
6
4
2
d)
Flexibility
4
3
2
1
Tropical Temperate
Tropical Temperate
Tropical Temperate
Tropical Temperate

**Fig. 3.3** Variation among habitat groups and biomes: **a)** mean density size spectra of epifauna within each habitat group and biome (ln(density) against ln(size bin mid-point)). Points represent density within a size bin for individual samples; grey shading represents 95% confidence intervals. Density by size data for turf and massive coral microhabitats (within habitat groups turfing algae and live coral, respectively) excluded animals <0.5 mm due to inaccurate sampling by suction. Y-axis breaks are presented on a $\log_{10}$ scale rather than $\log_e$ scale for ease of interpretation.

Box plots of variation in **b)** maximum height (cm), **c)** degree of branching, and **d)** relative flexibility among habitat groups and tropical and temperate biomes. Horizontal lines in each box plot represent, from top to bottom, third quartile, median and first quartile. The whiskers extend to 1.5 x interquartile range. Dots represent outliers. Asterisks indicate significant tropical/temperate differences ($0.01 < P < 0.001$).

**Table 3.5** Univariate PERMANOVA assessing effects of habitat group, biome (tropical or temperate), microhabitat (habitat group), location (biome), and all interaction terms on the slope of sample-level epifaunal size spectra. Nested factors are indicted by parentheses enclosing the factor in which they are nested. Effects highlighted in bold were retained in the final model at alpha <0.25. Negative values for percentage of variation explained by each factor are recorded as 0.

| Source of variation | Degrees of freedom | Mean square | Pseudo-*F* ratio | *P* value (by permutation) | % variation |
|---|---|---|---|---|---|
| **Habitat group** | **3** | **1.90** | **2.82** | **0.044** | **18.8** |
| **Microhabitat (Habitat group)** | **17** | **0.71** | **1.31** | **0.238** | **4.7** |
| **Biome** | **1** | **1.21** | **2.00** | **0.169** | **8.3** |
| Location (Biome) | 9 | 0.54 | 0.97 | 0.509 | 0 |
| **Habitat x Biome** | **3** | **1.34** | **1.82** | **0.124** | **5.0** |
| Microhabitat (Habitat group) x Biome | 7 | 0.69 | 1.33 | 0.270 | 20.7 |
| Habitat group x Location (Biome) | 11 | 0.55 | 1.04 | 0.447 | 0.6 |
| **Microhabitat (Habitat group) x Location (Biome)** | **25** | **0.56** | **1.53** | **0.109** | **9.4** |
| Residual | 75 | 0.36 | | | 32.5 |
| Total | 151 | | | | |

**Table 3.6** Univariate PERMANOVA assessing effects of terms for which P<0.25 in Table 4 on the slope of sample-level epifaunal size spectra. Final model included: habitat group, microhabitat (habitat group), biome, and interactions habitat group x biome, and microhabitat (habitat group) x location (biome). Nested factors are indicted by parentheses enclosing the factor in which they are nested. Effects highlighted in bold were significant at alpha <0.05.

| Source of variation | Degrees of freedom | Mean square | Pseudo-*F* ratio | *P* value (by permutation) | % variation |
|---|---|---|---|---|---|
| **Habitat group** | **3** | **3.56** | **5.13** | **0.003** | **17.3** |
| Microhabitat (Habitat group) | 17 | 0.77 | 1.37 | 0.220 | 3.7 |
| Biome | 1 | 1.16 | 2.13 | 0.153 | 2.6 |
| **Habitat x Biome** | **3** | **2.52** | **4.55** | **0.016** | **26.3** |
| Microhabitat (Habitat group) x Location (Biome) | 25 | 0.59 | 1.32 | 0.168 | 6.6 |
| Residual | 102 | 0.44 | | | 43.4 |
| Total | 151 | | | | |

Shifts in community composition along size spectra largely reflected changes in major crustacean groups – the dominant epifaunal taxa (Fig. 3.4). Harpacticoid copepods were the major contributors to the smallest size bins across all habitat groups, reaching highest proportions in the tropical biome. Peracarids were prevalent across a broad size range on macroalgae, particularly within the temperate biome. Peracarids were also important across a broad size range on the turf habitat group, whereas on sessile invertebrate and live coral habitat groups peracarids were most abundant in a reduced size range (0.5–2.8 mm on sessile invertebrates and 1–1.4 mm on live coral). Decapods dominated the largest size groups on the live coral habitat group with notable presence in the tropical biome, where they contributed most density from 2–8 mm. The ‘other invertebrates’ group tended to be more prevalent

within the temperate biome, with a contribution that varied among size groups and habitat groups.

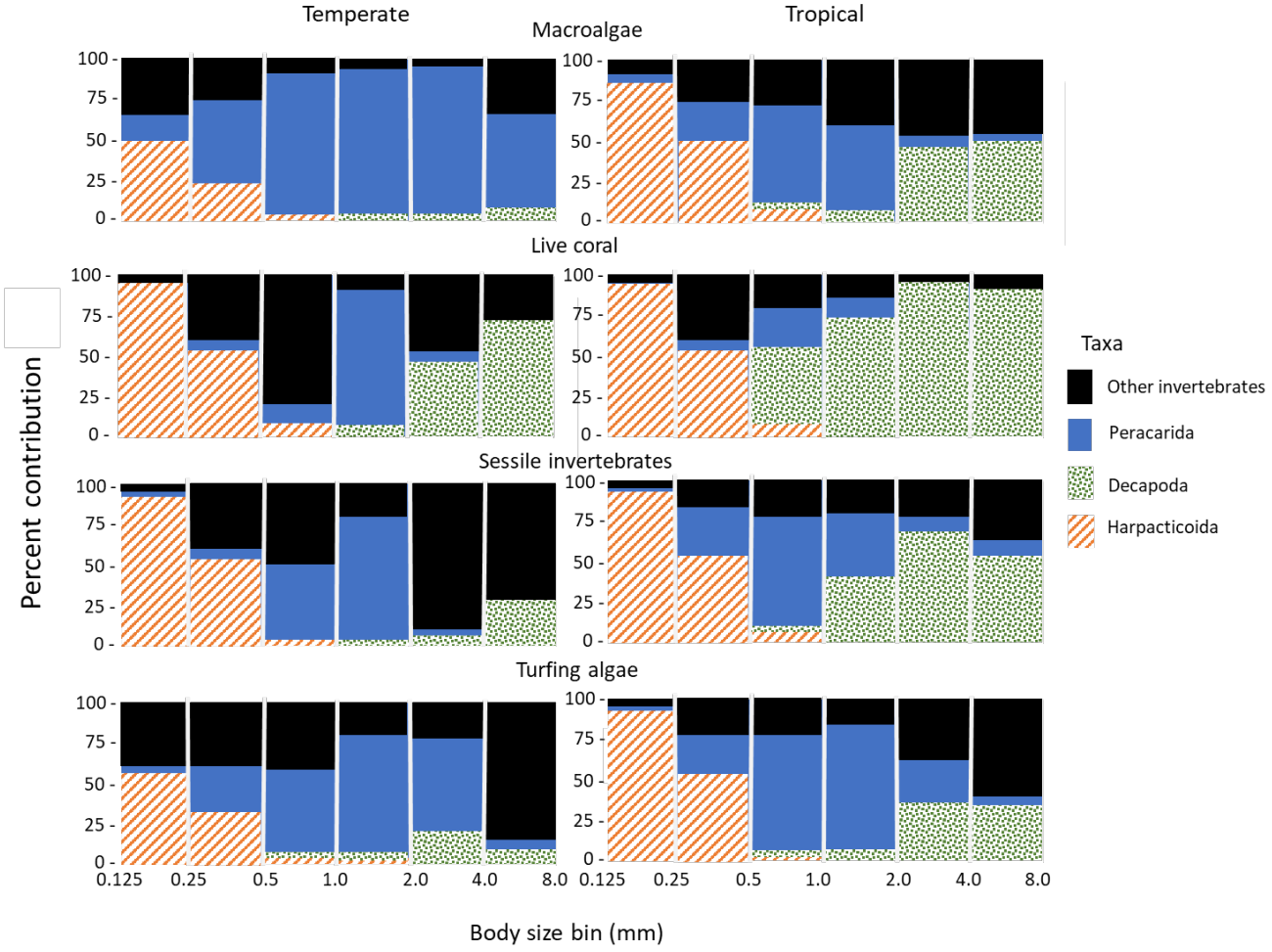



**Fig. 3.4** Percent contribution of four taxonomic groups (Decapoda, Peracarida, Harpacticoida and 'other invertebrates') to epifaunal density among size bins according to habitat group and biome.

## 3.6 Discussion

The community size spectrum for epifaunal invertebrates inhabiting eastern Australia's shallow reefs was remarkably consistent and linear when aggregated across observed local microhabitat mosaics at the scale of 50 m transects and plotted on a log-log scale. Comparing these estimates of epifaunal size spectra that accounted for local habitat variation, no

latitudinal pattern was apparent among reef locations across a substantial biogeographic gradient. Within each location, a linear model explained variation remarkably well ($R^2 \geq 0.8$). Similarly, size spectra were consistently linear (with one exception) when plotted among structurally heterogenous habitat groups ($R^2 \geq 0.6$). The results presented here support the hypothesis that epifaunal assemblage size spectra vary as a result of interactions between habitat type and climatic zone, since observed variation in size spectra between tropical and temperate biomes depended on the habitat group from which epifauna were collected. This suggests that any shifts in size spectra at this basal level of reef food webs, due to continuing climate change, will be predominantly mediated via changes in the availability of benthic habitats.

### 3.6.1 Habitat and size spectra variation

Epifaunal size spectra varied among habitat groups, eclipsing any tropical/temperate variation. When mean size spectra were estimated at the location level using proportional microhabitat cover at sampling sites, variation among locations reflected variation in microhabitat cover. The lack of biome effect suggested these differences in cover were more influential than environmental differences broadly associated with biomes.

A strong influence of habitat is unsurprising, given habitat structure at the scale appropriate to small epifaunal invertebrates has been identified as an important correlate of assemblage composition (Hacker and Steneck 1990, Gee and Warwick 1994a, Chemello and Milazzo 2002, Stella et al. 2010, Kramer et al. 2014, Marzinelli et al. 2014, Fraser et al. 2020a, Stelling-Wood et al. 2020) (Chapter 2). Despite the habitat-driven variation observed in epifaunal size spectra, both site- and sample-level size spectra were highly linear and, as expected, negatively sloped (Peters and Wassenberg 1983, Marquet et al. 1990). With one exception (described below), all size spectra closely fit a linear model ($R^2 \geq 0.6$). This

suggests that, if given a small size range of invertebrates in a sample, accurate prediction of invertebrate density in much smaller or larger size classes is possible.

The observed linearity and negative slope of epifaunal size spectra may be explained by metabolic rate scaling with body size. Herbivores comprise the predominant functional group within epifaunal assemblages, with microphytobenthos an important food source for invertebrates across the size spectrum (Edgar 1993). Kleiber's law states that the metabolic rate of an individual animal relates to the animal's mass by the power of 0.75 (Kleiber 1932). Thus, the rate of resource use (e.g. microphytobenthic food) by an individual is relative to its body mass, and this rate scales with body mass. Although Kleiber's law refers to mass, the same concept can be applied to other metrics of body size, although the exact power ratio may vary (Trebilco et al. 2016). Individuals in smaller size classes will require a smaller amount of food so, assuming sufficient food resources are available, one can expect density to decrease as body size increases (Damuth 1981), often at a scale reciprocal to metabolic rate increase (Damuth 1991). Linear size spectra (log-log scale) are generally observed in oligotrophic ecosystems that have not recently experienced major disturbance (Marquet et al. 2005), as well as eutrophic ecosystems dominated by herbivores (Damuth 1981). Common processes that interfere with expected linearity and slope of size spectra include size-selective predation (Rassoulzadegan and Sheldon 1986, Sheldon et al. 1986), and metabolic inefficiencies in the transfer of energy if individuals in larger size bins feed upon those in smaller size bins (Lindeman 1942, Trebilco et al. 2013). Hence, a steeper slope may be expected within a trophic group if predators target larger individuals, or if intra-group predation occurs.

Among habitat groups sampled here, the steepest size spectra were observed on macroalgae and turfing algae habitats. Macroalgae- and turfing algae-associated assemblages were characterised by relatively high densities of invertebrates in the smallest size classes and

relatively low densities in the largest size classes. Small size classes on these habitats were dominated by harpacticoid copepods, whereas taxonomic contributions to large size classes varied between macroalgae and turf, and tropical and temperate biomes.

Macroalgae thalli often host epiphytic microphytobenthos including diatom-dominated films and fine filamentous algae (Poore et al. 2012), providing substantial food resources for herbivorous epifauna. Turfing algae may be directly consumed by herbivorous epifauna, and turf effectively traps detritus (Connell et al. 2014), providing food for detritivores, another important functional group common in epifaunal assemblages (Kramer et al. 2012). Hence, linear epifaunal size spectra may be expected in association with these habitats. Size-selective predation may also contribute to relatively steep slopes on these habitats. The structure of macroalgae and turfing algae is relatively flexible compared with live coral and sessile invertebrates (Fig. 3.3d), allowing benthic invertivores to easily penetrate in order to extract larger, visible prey items (Hixon and Jones 2005). The presence of micro-carnivores within these epifaunal assemblages may also influence the slope, but the functional composition of assemblages has not been considered here.

By contrast, live coral-associated assemblages showed much flatter size spectra than the algal habitat groups, with considerably lower invertebrate densities in the smallest size classes and marginally higher densities in the largest size classes. Harpacticoid copepods comprised >90% of epifauna in the smallest size classes on live coral, with decapods dominating the largest size classes. Predation by large epifauna on animals in smaller size bins is less likely on live coral than on algal habitats, given the lower size spectrum intercept observed on these habitats (Lindeman 1942, Trebilco et al. 2013).

Epifauna on sessile invertebrate habitats possessed size spectra that generally fell mid-way between algal habitats and live coral, with relatively high invertebrate densities in the largest

size classes and moderate densities in the smallest size classes. As was the case for live coral habitats, the smallest size classes on sessile invertebrate habitats comprised >90% harpacticoid copepods with the largest size classes dominated by decapods in tropical samples and the ‘other invertebrates’ group in temperate samples.

As well as possessing flatter size spectra, epifaunal assemblages inhabiting tropical live coral represented an exception to size spectra linearity (Fig. 3.3a; $R^2 = 0.37$). This suggests the live coral habitat group is favourable to particular epifaunal size classes. With the exception of massive corals, it is likely that the rigid, often complex structure of live coral limits predator access to epifauna, providing size-dependent refuge for larger invertebrates (Kramer et al. 2016). Predation by corals may also partly explain the lower densities of small epifauna on live coral, as coral polyps can consume very small invertebrates (Goreau et al. 1971, Gochfeld 2004, Houlbréque and Ferrier-Pagés 2009). Some larger decapods consume food resources directly associated with live coral, such as coral mucus or particles trapped by coral polyps (Galil 1987), making live coral habitat preferable to these animals. By contrast, live coral habitat offers minimal microphytobenthic food to herbivorous epifauna (Yamashiro et al. 2012), which may influence the relative paucity of small and mid-sized invertebrates in these assemblages (Edgar 1993).

The predictable relationship between habitat group and epifaunal size spectra provides useful information for estimates of size spectra shifts in response to reef habitat transformation. If benthic habitat availability can be accurately mapped and changes documented or predicted, the availability and size structure of the epifaunal food source within reef food webs may be estimated, with consideration of the habitat group x biome interaction adding further accuracy.

### 3.6.2 Interactive influences of habitat and climate

The interaction between the effects of habitat and biome on size spectra slopes suggested temperate-tropical differences among samples in the macroalgal and sessile invertebrate habitat groups (Fig. 3.3a). Epifauna associated with macroalgae from tropical reefs had a steeper assemblage size spectrum than those from the same habitat group from temperate reefs. In fact, the size spectrum of epifauna on tropical macroalgae was most similar to the epifaunal size spectrum of tropical turf samples. Epifaunal size spectra slopes in sessile invertebrate habitats were slightly steeper in temperate samples, and epifaunal densities also tended to be higher across size classes.

On one hand, size spectra differences between temperate and tropical samples for these broader habitat groups could be confounded by temperate-tropical differences in the microhabitats that make up the broader habitat. For example, the sessile invertebrate habitat included a combination of soft corals and sponges, with samples from tropical reefs comprising 57% soft coral and 43% sponges, whereas 100% of samples from temperate reefs in this habitat group comprised sponge microhabitats. Likewise, large laminarian kelps only contributed to the macroalgal habitat in temperate samples. Such confounding is unlikely to be solely responsible for the significant interaction, however, as the non-significant effect of microhabitat on size spectra slopes (Tables 3.5, 3.6) suggests that epifaunal size spectra did not vary significantly between soft corals and sponges or the various macroalgal microhabitats.

Instead, structural differences between the microhabitats sampled in the temperate and tropical locations appear to provide a more direct explanation, probably mediated by variation (albeit non-significant) between microhabitats. Macroalgal samples collected from temperate reefs were taller and more branched than tropical macroalgal samples, likely

supporting more large epifauna through reduced exposure to predators (and consequently reduced small epifauna through resource constraints) (Edgar 1994). In contrast to macroalgae, sessile invertebrate microhabitats were shorter on temperate reefs, hosting epifauna with a steeper assemblage size spectrum than on tropical reefs. Similar slopes of epifauna in tropical macroalgae and tropical turfs were also reflected in similarities in the degree of branching and height between macroalgae and turfs from tropical reefs, further suggesting that microhabitat height may be an important influence on epifaunal size structure. Tropical/temperate differences in size spectra slopes on select habitats may also be related to variation in the trophic status of reef ecosystems (Sprules and Munawar 1986), assuming tropical reefs sampled here were generally more oligotrophic, and temperate reefs more eutrophic (McClanahan et al. 2002a, Burkepile and Hay 2006). Theoretically, in eutrophic systems, nutrients enter the food web at a high rate and are cycled rapidly through grazers in smaller size classes to produce relatively high densities in larger size classes. In oligotrophic systems, by contrast, nutrients enter the food web at a lower rate and slower cycling through small grazers produces fewer grazers in larger size classes (Sprules and Munawar 1986).

Notably, a large residual error remained in both site- and sample-level analyses after accounting for the variation associated with tested covariates and their interactions (Tables 3.4, 3.6). This may be a product of unexplained ecological or environmental factors that *a priori* were not considered important, such as biomass of benthic predators or habitat transforming taxa (e.g. herbivores or corallivores), depth, wave exposure, or human impacts. The large residual error may also be a result of stochastic noise in the data, due to the broad biogeographic study area and opportunistic sampling approach. Of great overarching significance, however, is that the size spectrum apparently represents an emergent macro-ecological property that is not greatly affected by local environmental factors. Regardless, a

sufficiently strong signal exists to assume habitat influences epifaunal size spectra, and that tropical/temperate variation largely depends on habitat.

### 3.6.3 Implications for climate change predictions

Globally, reef ecosystems are undergoing dramatic changes, with widespread transformation of benthic habitats. Given the clear correlation between epifaunal size spectra and structurally diverse habitats, and the size-specific predation of many benthic invertivores (Edgar and Aoki 1993, Kramer et al. 2015), ongoing shifts in available reef habitats are likely to substantially influence basal food web dynamics. The epifaunal size spectrum on coral-dominated reefs will likely steepen following decline in live coral and increased cover of turf algae and/or macroalgae habitats (Mumby et al. 2007b, Nelson et al. 2016, O'Brien and Scheibling 2018), with less food available for invertivores favouring larger decapods and considerably more food available for those favouring small harpacticoid copepods and mid-sized peracarids. In contrast, if reefs historically dominated by macroalgae transform towards higher cover of turfing algae (Filbee-Dexter and Wernberg 2018, O'Brien and Scheibling 2018, Reeves et al. 2018), epifaunal size spectra may not change much. This suggests resource availability for benthic invertivores may be maintained on temperate reefs assuming succession towards turfing algae. If, however, substantial cover of live coral succeeds macroalgae, as described by Ling et al. (2018a), epifaunal size spectra may flatten significantly, with dramatic declines in small harpacticoid copepod prey. Increased availability of larger decapod prey may be less widespread in this scenario, depending on the complexity of live corals and subsequent refugia for larger epifauna.

Body-size distribution is often overlooked in studies of community structure, with comparisons of faunal diversity, taxonomic composition, density and biomass more common (Berthelsen et al. 2015, Cúrdia et al. 2015, Desmond et al. 2018). However, results presented

here reveal highly predictable properties with regards to the size spectra of epifaunal assemblages on diverse benthic habitats. Without consideration of size spectra, comparisons of total density or biomass of epifauna would be confounded and largely meaningless, as outcomes would vary considerably depending on the size of animals sampled. For example, using data presented here, density comparisons of epifauna ≥1 mm body size between macroalgae and live coral habitat groups will draw opposite conclusions to the same comparison using epifauna <1 mm (see Fig. 3.3a).

Given the crucial role epifaunal invertebrates play in shallow reef food webs and the assumption that predation patterns vary with epifaunal body size (Edgar and Aoki 1993, Kramer et al. 2015), consideration of epifaunal size spectra is fundamental for understanding potential changes at basal levels of reef food webs as reef habitats transform. The critical nature of information provided by size spectra data likely extends to studies of other faunal communities. For example, comparisons of total fish density inside and outside marine reserves may produce contradictory results, depending on the distribution of body sizes. Thus, results presented here highlight faunal size spectra as an important consideration in future ecological research, particularly for research involving food web dynamics.

## 3.7 Acknowledgements

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## 3.8 Supplementary material

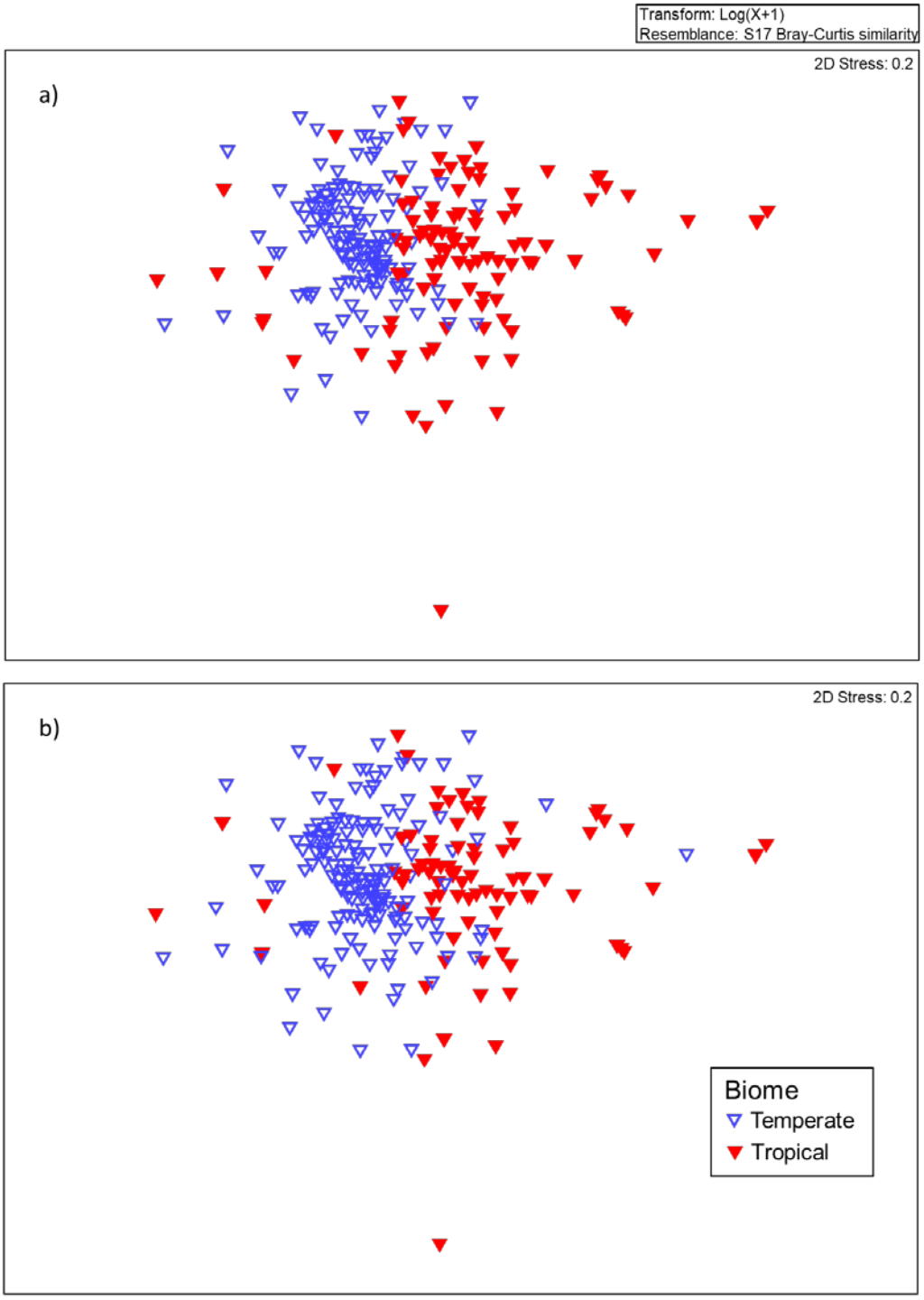


**Fig. 3.5 (S1)** Non-metric multidimensional scaling (nMDS) ordination showing samples clustered according to similarity of epifaunal taxonomic composition. Symbols represent biomes and samples from the Solitary Islands were grouped with samples from **(a)** tropical locations and **(b)** temperate locations.

**Table 3.7 (S1)** Multivariate PERMANOVA assessing variation in taxonomic composition of epifaunal assemblages among microhabitats, sampling locations, and biomes with **(a)** Solitary Islands grouped with tropical locations, and **(b)** temperate locations.

| Source of variation | Degrees of freedom | Sum of squares | Mean square | Pseudo-*F* ratio | *P* value (by permutation) |
|---|---|---|---|---|---|
| a) Solitary Islands in Tropical Biome | | | | | |
| Biome | 1 | 10945 | 10945 | 2.65 | 0.001 |
| Location (Biome) | 10 | 66297 | 6630 | 2.73 | 0.001 |
| Microhabitat | 27 | 168950 | 6257 | 1.67 | 0.001 |
| Biome x Microhabitat | 7 | 27619 | 3946 | 1.12 | 0.229 |
| Location (Biome) x Microhabitat | 45 | 165120 | 3669 | 1.51 | 0.001 |
| Residuals | 147 | 356450 | 2425 | | |
| Total | 237 | 911800 | | | |
| b) Solitary Islands in Temperate Biome | | | | | |
| Biome | 1 | 14745 | 14745 | 3.01 | 0.001 |
| Location (Biome) | 10 | 71320 | 7132 | 2.94 | 0.001 |
| Microhabitat | 27 | 166310 | 6160 | 1.65 | 0.002 |
| Biome x Microhabitat | 10 | 38553 | 3855 | 1.12 | 0.265 |
| Location (Biome) x Microhabitat | 42 | 153040 | 3644 | 1.50 | 0.001 |
| Residuals | 147 | 356450 | 2425 | | |
| Total | 237 | 911800 | | | |

# Chapter 4

# HIGH BIOMASS AND PRODUCTIVITY OF EPIFAUNAL INVERTEBRATES LIVING AMONGST DEAD CORAL

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**Preface:**

*This paper is in review at Coral Reefs:*

Fraser KM, Stuart-Smith RD, Ling SD, Edgar GJ (*in review*) High biomass and productivity of epifaunal invertebrates living amongst dead coral

In Chapter 4 I conduct a case study of subtropical and tropical reefs, comparing the epifaunal assemblages inhabiting live branching coral and dead, turf-covered coral: habitats that broadly represent ‘healthy’ and ‘degraded’ coral reefs. Chapters 2 and 3 revealed stark differences in the taxonomic composition and size structure of assemblages hosted by these two habitats. Chapter 4 builds on Chapters 2 and 3 by comparing the density, biomass, and productivity, as well as the taxonomic composition and size structure of epifauna on live and dead coral, suggesting potential outcomes for coral reef food webs under conditions of habitat ‘collapse’ or transformation. Chapter 4 leads into Chapter 5 by indicating clear differences between two important habitat groups in terms of a range of epifaunal assemblage metrics, and by showing a lack of variation in these metrics among the four subtropical and tropical reef locations.

## 4.1 Abstract

Climate change is transforming coral reef structures, with important yet largely unknown consequences for reef food webs. Crustaceans, molluscs, polychaetes, and other small motile invertebrates living as epifauna on coral habitats represent an essential trophic link between primary producers and a diverse and abundant invertivorous fish fauna. Here, we investigate variation in assemblages of motile epifaunal invertebrates on live coral and dead coral heavily overgrown by turf algae. Sampling was conducted at four eastern Australian locations – along the northern and central Great Barrier Reef, and, adjacent to the central east coast, the Solitary Islands and offshore Elizabeth and Middleton Reefs. Epifaunal assemblages differed significantly between live and dead 'turf-covered' coral habitats, with overall density, biomass, and productivity of epifauna more than an order of magnitude greater on dead than on live coral. The size structure and composition of assemblages also differed: turf-covered dead coral supported greater abundances of small animals than live coral, notably harpacticoid copepods, while live coral assemblages had proportionately greater abundances of larger decapods. A ten-fold increase in secondary productivity of motile invertebrates is predicted as live corals are replaced by turf-covered dead coral, however this productivity will predominantly be available as small harpacticoid copepod prey (size range: 0.125–0.25 mm). Associated flow-on effects through reef food webs are likely, as changes to epifauna will directly affect invertivore communities, which will, in turn, influence larger carnivores and other associated functional groups.

## 4.2 Keywords

coral reefs, climate change, macrofauna, food web, phase shift, size structure

## 4.3 Introduction

Climate change is transforming coral reef ecosystems worldwide through increasing frequency and severity of heat-induced coral bleaching events (Hughes et al. 2017b) and increasing intensity of tropical storms (Cheal et al. 2017). Corals that do not recover from bleaching become overgrown with turfing algae and break down into turf-covered rubble (Nelson et al. 2016, O'Brien and Scheibling 2018), a process accelerated by storm disturbance (Kobluk and Lysenko 1987, Cheal et al. 2017). Climate change predictions suggest coral reef degradation will continue to increase (Hughes et al. 2017a, Bindoff et al. 2019), with significant implications for reef fauna, food webs, and ultimately reef ecosystem structure.

Small motile invertebrates comprise the highest density and diversity of animals directly associated with coral reef substrates (Plaisance et al. 2011), providing substantial biomass and productivity to reef food webs (Kramer et al. 2017). Epifaunal invertebrates, ranging in size from macroscopic (i.e. >1 cm) to microscopic (≤1 mm), are ubiquitous inhabitants of the surfaces of reef structures, while another group – the cryptobenthic invertebrates – inhabit the interstices within the coral reef framework (Enochs and Hockensmith 2008). Live, healthy corals support abundant assemblages of epifauna including obligate symbionts and associates (Glynn 2011). Structurally diverse species of live coral often host taxonomically distinct epifauna (Stella et al. 2010), with greater variation observed among individual coral heads than among reef sites (Counsell et al. 2018). Dead coral structures also host abundant assemblages of epifauna, however the taxonomic composition of assemblages inhabiting dead coral can differ considerably from those inhabiting live coral (Kramer et al. 2014, Nelson et al. 2016, González-Gómez et al. 2018, Fraser et al. 2020a). The fine-scale structure of the immediate habitat is a major driver of variation in epifaunal assemblages (Kramer et al. 2014, Fraser et al. 2020a) (Chapter 2), often due to a combination of complexity (Enochs et

al. 2011, Enochs 2012), surface area (Preston and Doherty 1994), and the diversity of 'nano-habitats' at scales available to invertebrates across a range of body sizes (Klumpp et al. 1988, Glynn and Enochs 2011).

Coral mortality and the transformation of coral reef-scapes from live coral dominance towards turf-covered dead coral and coral rubble will likely have substantial impacts on epifaunal invertebrate assemblages. Coral mortality has been shown to affect the ecological interactions among obligate live coral-associated decapods large enough for in-situ or aquarium-based visual census and observation (Stella et al. 2014), resulting in decreased density and fecundity of some species (Stella et al. 2011) and potentially leading to extinctions (Glynn 2011). Epifaunal assemblages associated with living corals are often characterised by these macroscopic decapods (Abele and Patton 1976, Stella et al. 2010, Kramer et al. 2014). In contrast, dead coral and coral rubble tend to host assemblages characterised by a greater diversity of taxa, including amphipods, decapods, cumaceans, tanaids and harpacticoid copepods (Klumpp et al. 1988, Kramer et al. 2014). Assemblage-based studies have suggested dead coral can support significantly higher abundances of epifauna than live coral, despite relatively few visible decapod species (Kramer et al. 2014, Nelson et al. 2016).

Epifaunal invertebrates play a crucial secondary productivity role in shallow reef food webs (Edgar 1990b), by which they link benthic primary producers and invertivores (Edgar and Moore 1986, Taylor 1998, Kramer et al. 2013), which represent among most prolific trophic groups on coral reefs (Kramer et al. 2015). As such, it is important to quantify epifaunal assemblages using metrics that represent their availability as a food source. Epifaunal density, biomass and productivity provide useful metrics for understanding energy transfer via benthic pathways. These metrics alone, however, are inadequate for accurate predictions of energy transfer via epifauna, as predation and consumption patterns vary considerably depending on

epifaunal body size, behaviour and palatability (Edgar and Aoki 1993, Kramer et al. 2015). Epifaunal crustacean taxa have been examined in relation to variation in density, biomass and productivity among coral reef habitats (Kramer et al. 2014), and biomass and productivity calculations are generally based on some measure of body size multiplied by abundance (Edgar 1990b). Community size structure itself, however, may provide a more broadly applicable indication of availability of epifaunal assemblages as prey, and may differ markedly between live and dead coral. Community size structure is often quantified by the slope of the size spectrum: the linear relationship between log abundance (or log biomass or log productivity) and body size, regardless of taxonomic identity (White et al. 2007, Edwards et al. 2017). The steepness of the slope indicates variation in abundance (or biomass or productivity) within the assemblage attributed to larger versus smaller animals (Trebilco et al. 2015). Understanding the contribution of different sized epifauna to density, biomass and productivity of assemblages is critical for predicting variation in the availability of food for benthic invertivores on coral reefs, given species-specific variation in food-size preferences among invertivorous fishes (Kramer et al. 2015).

Here we compare epifaunal invertebrate assemblages (0.125 – 22 mm body size) associated with live and dead coral from four locations broadly spanning the distribution of corals on the eastern seaboard of Australia. Given our overarching aim of understanding consequences of the loss of live corals, we test the hypotheses that: 1) turf-covered dead coral generally supports significantly higher density, biomass and productivity of epifaunal invertebrates than live coral; and 2) the composition of the epifaunal assemblage and its size-structure differs between turf-covered dead coral and live coral, with live coral hosting proportionally more larger decapods and shallower size spectrum slope, and turf-covered dead coral hosting proportionally more smaller taxa such as amphipods and harpacticoid copepods and a steeper size spectrum slope.

## 4.4 Materials and methods

### 4.4.1 **Study area and sample collection**

Shallow reefs were sampled during the period February to November 2018 at four distinct locations across the range of coral reefs in eastern Australia, including Lizard Island on the northern Great Barrier Reef (GBR), Whitsunday Islands on the central GBR, the offshore subtropical Elizabeth and Middleton atolls, and subtropical Solitary Islands (Fig. 4.1). A total of 40 epifaunal samples sourced from live and dead coral were collected. Additional epifaunal samples were collected in association with other habitat types (e.g. macroalgae, sponges), as analysed and discussed elsewhere (Fraser et al., 2020) (Chapter 2). Samples from both live and dead coral were collected randomly across a depth range of 1 – 10 m. Sampling was conducted in relatively sheltered zones (e.g. lagoonal reefs, leeward reef slopes, and leeward sides of islands to prevailing swell directions).

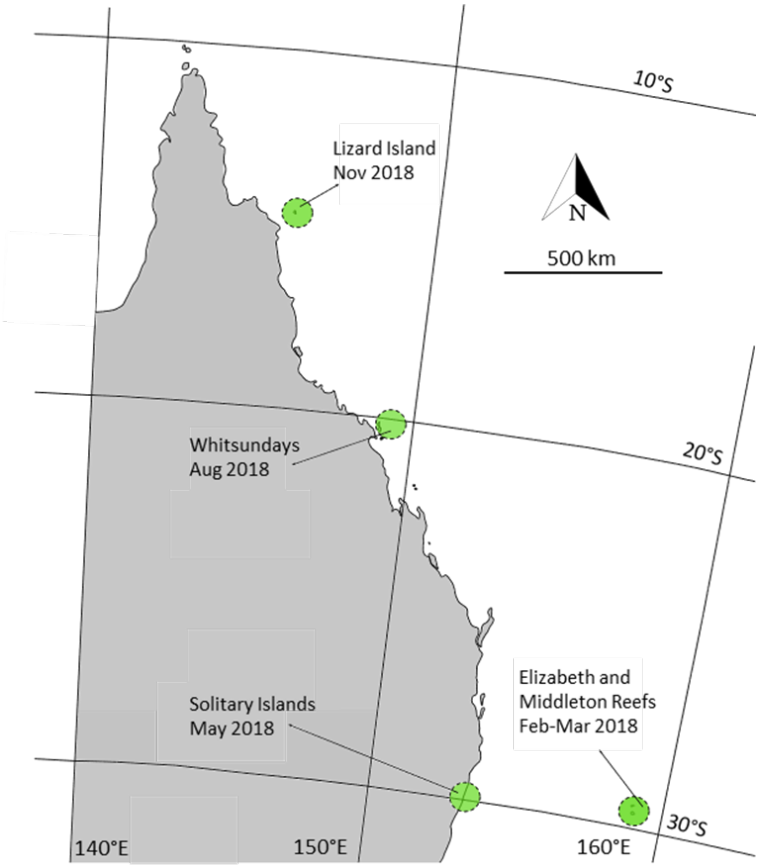


**Fig. 4.1** Map of eastern Australian sampling locations showing month sampling was performed during 2018.

Sampling involved haphazard SCUBA-based collection of epifauna associated with 6 different live and dead coral microhabitats. Samples were categorised into microhabitats according to taxonomy and morphology (Table 4.1), following previous studies to classify reef habitat types (Cresswell et al. 2017) and by the CATAMI scheme (Althaus et al. 2015). CATAMI provides an Australian national standard for benthic habitat classification. Microhabitats were selected for sampling as they were sighted, ensuring samples were separated by >5 m on the reef. Each microhabitat was categorised more coarsely as either live or dead coral (Table 4.1).

**Table 4.1** Microhabitats sampled, with live or dead coral classification, sample size (parentheses contain the number of total samples collected at each location; LI = Lizard Island, Whit = Whitsundays, EMR = Elizabeth and Middleton Reefs, Sol = Solitary Islands), description, and example genera.

| **Microhabitat category** | **Live or dead coral** | **Number of samples** | **Description** | **Example genera** |
|---|---|---|---|---|
| Pocillopora | Live coral | 9 (LI = 3, Whit = 2, EMR = 2, Sol = 2) | Stony corals forming branching colonies, genus Pocillopora | *Pocillopora* |
| Branching Acropora | Live coral | 6 (Whit = 1, EMR = 3, Sol = 2) * | Stony corals forming branching colonies, genus Acropora | Acropora |
| Tabula Acropora | Live coral | 3 (EMR = 3) * | Stony branching corals forming tabular colonies, genus Acropora | Acropora |
| Other branching/erect coral | Live coral | 8 (LI = 2, Whit = 1, EMR = 4) | Fine or robust branching, columnar or foliaceous stony coral colonies | Seriatopora, Stylopora |
| Erect dead coral | Dead coral | 9 (LI = 3, Whit = 2, EMR = 3, Sol = 1) | Dead erect coral skeleton overgrown predominantly by fine filamentous turfing algae | Acropora (dead), Pocillopora (dead) |
| Coral rubble | Dead coral | 5 (LI = 3, EMR = 2) | Broken dead coral rubble overgrown predominantly by fine filamentous turfing algae | Acropora (dead), Pocillopora (dead), Porites (dead) |

Prior to collection, a 25 cm x 25 cm grid-subdivided quadrat was placed over the selected sample and photographed to quantify the planar area of sampled habitat. Erect live and dead

corals were enclosed in plastic 22 x 22 cm zip-lock bags, chiselled off the reef, and bags immediately sealed following Stella et al. (2010). Coral rubble was collected by hand by placing a zip-lock bag over the hand, collecting coral rubble, and immediately sealing the bag. Highly motile epifauna may have escaped using this approach. All samples within sealed zip-lock bags were transported to a boat, where they were immediately flushed three times in fresh water to remove motile invertebrates. Flushing involved placing samples in a sorting tray, covering with fresh water and agitating for 1 minute, following Stella et al. (2010), before the water and dislodged invertebrates were poured through a 125 µm sieve. This method excluded boring invertebrates; therefore, complete coral-associated invertebrate assemblages are likely to differ from those discussed here. After three flushes, invertebrates retained on the sieve were transferred to a 70 mL sample jar and fixed in 5% buffered formalin solution. Dead coral and coral rubble samples were returned to the reef and placed within rubble beds. Immediately after removing epifauna, live coral samples were re-immersed in seawater and re-attached to their colonies where possible (or to nearby substrate) using marine epoxy putty following Stella et al. (2010).

### 4.4.2 Laboratory processing

Invertebrates from each sample were washed of formalin and passed through a nested series of 12 sieves stacked in descending order of mesh size, following a $\log_{\sqrt{2}}$ series (5.6, 4.0, 2.8, 2.0, 1.4, 1.0, 0.71, 0.5, 0.355, 0.25, 0.18, 0.125 mm, after  Animals retained on each sieve were washed into petri dishes for identification and counted under a dissecting microscope, with data binned by sieve mesh size. Identification of epifauna was performed to order-level where possible, otherwise to phylum (<2% of animals). Animals retained on the 5.6 mm sieve were measured with calipers at their widest dimension and counts placed into additional $\log_{\sqrt{2}}$ size bins (8, 11, 16, 22 mm).

### 4.4.3 Data analysis

Preliminary analyses contrasted order-level taxonomic composition among microhabitats nested within coarse categories ‘live coral’ and ‘dead coral’ using the PERMANOVA add-on in Primer 7 (Clarke and Gorley 2015). Results indicated relative homogeneity in epifaunal communities associated with the different coral microhabitats grouped as live or dead coral ($P$ >0.05; Table 4.2), with significant variation between coarse categories ‘live coral’ and ‘dead coral’ ($P$ ≤0.001; Table 4.2). Larger sample sizes within live and dead coral categories provided greater statistical power than when samples were separated according to finer microhabitats, consequently microhabitats have not been considered further. Moreover, previous field research has identified similar assemblages of epifaunal crustaceans associated with erect dead coral and coral rubble (Kramer et al. 2014).

#### *4.4.3.1 Density, biomass, and productivity*

Given that strong relationships exist between epifaunal biomass and light (Edgar 1993), which is ultimately a planar metric, epifaunal abundance by taxa and size were standardised to 1 $m^2$ planar area (density) (Fraser et al. 2020a) (Chapter 2), accounting for the area of sampled microhabitat photographed underwater prior to collection. Standardisation by planar area also allows comparison of epifaunal assemblage metrics to densities of other trophic groups (e.g. primary producers, benthic invertebrates, fishes), which are typically expressed per square metre of seabed. Moreover, standardisation of habitats in other ways generates bias towards species that respond to a particular habitat feature (Edgar 1983).

Epifaunal biomass as ash-free dry weight (AFDW) of individuals within each size bin was derived from published estimates of mean biomass across macrofaunal taxonomic groups (Edgar 1990b). Productivity estimates were calculated using the general allometric equation given by Edgar (1990b):

$$P = (10\text{^}((-2.31 + 0.8 * \log10(\mathrm{B} * 1000) + 0.89 * \log10\mathrm{T}))/1000$$

where *P* is productivity of an individual (mg AFDW $d^{-1}$), *B* is the biomass of an individual (mg AFDW), and *T* is water temperature (°C) at the time of sampling. Biomass and productivity estimates of individual animals were then summed to provide total biomass (mg AFDW $m^{-2}$) and total productivity estimates (mg AFDW $m^{-2}$ $d^{-1}$) for each sample. We note that this method for estimating biomass and productivity was originally established for individuals ≥0.5 mm; here we assume the equations used by Edgar (1990b) also apply to smaller individuals (≥0.125 mm) based on linear extrapolation of well-supported trends (i.e. $R^2$ ranging from 0.87 to 0.98 (Fraser et al. 2020c) (Chapter 3)).

The influence of habitat (live vs. dead coral) and location on total density, biomass and productivity of epifaunal assemblages per $m^2$ were assessed using univariate permutational analyses of variance in Primer 7 (PERMANOVA; (Anderson 2001, McArdle and Anderson 2001, Clarke and Gorley 2015, Anderson 2017)) on Euclidean distance resemblance matrices of log(x+1) transformed density, biomass, and productivity data.

#### *4.4.3.2 Assemblage size spectra*

Density, biomass, and productivity data for each sample were partitioned into sieve mesh size bins. For each sample, the slopes for density, biomass, and productivity size spectra were calculated using linear regression ($\log_{10}$(density, biomass, or productivity) against $\log_{10}$(mid-point of each size bin)) in R (R Core Team 2019) and the *tidyverse* package (Edwards et al. 2017, Wickam et al. 2019). Mean size spectra were plotted for live coral and dead coral using the same packages, with $R^2$ values indicating the consistency in size spectra among samples. Variation in $R^2$ values for each size spectrum represents a general ecological indicator of consistency among samples, rather than a statistical indicator given the points related to each

sample are not independent. Zero counts in larger size bins affected the linear fit of data, therefore data were included up to the largest size bin in which animals were present.

Variation in sample-level size spectra slopes between live coral and dead coral was examined using univariate permutational analysis of variance ((PERMANOVA; (Anderson 2001, McArdle and Anderson 2001, Anderson 2017)).

#### *4.4.3.3 Taxonomic composition*

Multivariate community analyses were conducted using PRIMER 7 (Clarke and Gorley 2015). A permutational analysis of variance (PERMANOVA; (Anderson 2001, McArdle and Anderson 2001, Anderson 2017)) was conducted on a Bray-Curtis resemblance matrix of $\log_{10}$ (x+1) transformed density, biomass and productivity data by taxa to test for assemblage differences between live and dead coral.

Pairwise PERMANOVA was used to make comparisons between epifauna associated with live and dead coral. Similarity percentages analysis (SIMPER; (Clarke 1993)) of density data was used to identify taxa most influential to dissimilarity among epifauna associated with the two habitats. Mean percent composition of these influential taxa (with additional taxa grouped as 'other') inhabiting live and dead coral was visualised using stacked bar charts in R (R Core Team 2019) and the *tidyverse* package (Wickam et al. 2019).

## 4.5 Results

### 4.5.1 Epifaunal communities associated with live versus dead coral

No significant variation was evident in epifaunal assemblages among sampling locations, with regards to overall density, biomass, productivity, or taxonomic composition ($P$ >0.05; Tables 4.2, 4.3, Fig. 4.2). Consequently, location was omitted from all subsequent analyses by testing hypotheses based on data pooled within live or dead coral across all locations. Epifaunal assemblages associated with live and dead coral were significantly different, with

overall density, biomass, and productivity of epifauna more than an order of magnitude greater on dead than on live coral habitat (Fig. 4.2; Table 4.3).

**Table 4.2** Multivariate PERMANOVA assessing effects of live vs. dead coral, location, microhabitat (nested within live vs. dead coral), and interactions between live vs. dead coral and location, and microhabitat (nested with live vs. dead coral) and location on the order-level composition of epifaunal assemblages. Effects highlighted in bold were significant at $\alpha$ <0.05.

| Source of variation | Degrees of freedom | Mean square | Pseudo-*F* ratio | *P*-value (by permutation) |
|---|---|---|---|---|
| **Live/Dead** | **1** | **9248** | **7.51** | **0.001** |
| Microhabitat (Live/Dead) | 4 | 923 | 0.85 | 0.632 |
| Location | 3 | 1072 | 1.04 | 0.459 |
| Live/Dead x Location | 3 | 818 | 0.79 | 0.618 |
| Microhabitat x Location | 5 | 1054 | 1.70 | 0.056 |
| Residual | 23 | 619 | | |
| Total | 39 | | | |

**Table 4.3** PERMANOVA table assessing differences in overall assemblage density, biomass, and daily productivity on live and dead coral habitats, among sampling locations, and under the interacting effects of live vs. dead coral and location. Live vs. dead coral habitat is a fixed factor, location is random. Effects highlighted in bold were significant at $\alpha$ <0.05.

| Source of variation | Degrees of freedom | Mean square | Pseudo *F*-value | *P*-value |
|---|---|---|---|---|
| Density | | | | |
| **Live/Dead** | **1** | **110.87** | **52.70** | **<0.05** |
| Location | 3 | 1.48 | 0.44 | 0.707 |
| Live/Dead x Location | 3 | 1.76 | 0.52 | 0.621 |
| Residuals | 32 | 3.36 | | |

| | | | | |
|---|---|---|---|---|
| Biomass | | | | |
| **Live/Dead** | **1** | **55.73** | **105.17** | **<0.05** |
| Location | 3 | 0.77 | 0.33 | 0.784 |
| Live/Dead x Location | 3 | 0.05 | 0.02 | 0.995 |
| Residuals | 32 | 2.31 | | |
| Productivity | | | | |
| **Live/Dead** | **1** | **42.49** | **161.22** | **<0.01** |
| Location | 3 | 0.17 | 0.17 | 0.920 |
| Live/Dead x Location | 3 | 0.06 | 0.06 | 0.977 |
| Residuals | 32 | 1.00 | | |

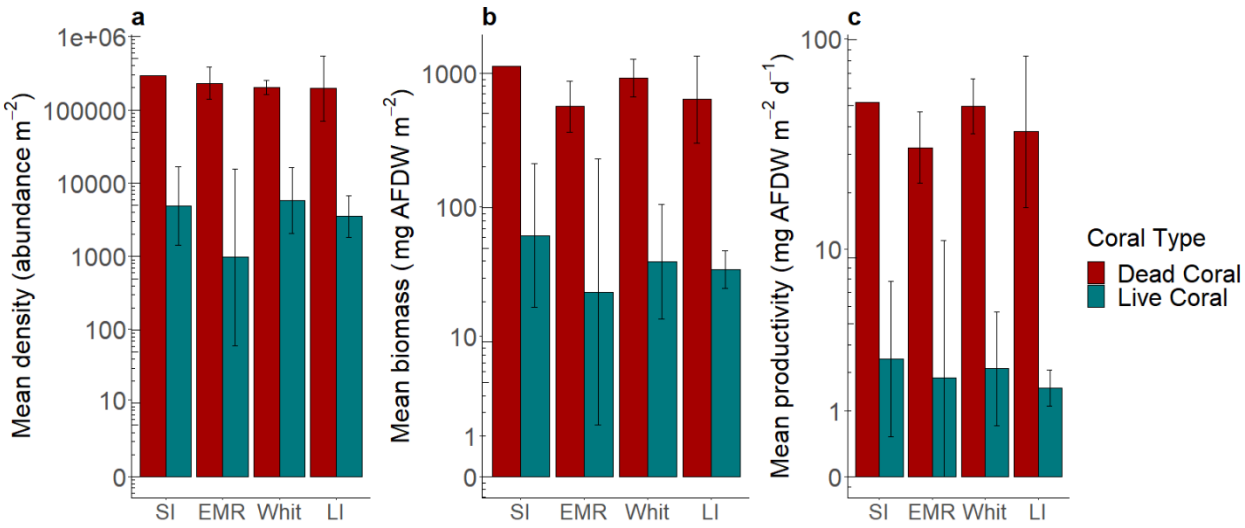


**Fig. 4.2** Mean **(a)** density (abundance m$^{-2}$), **(b)** estimated biomass (mg AFDW m$^{-2}$), and **(c)** estimated daily productivity (mg AFDW m$^{-2}$ d$^{-1}$) of epifauna within 1 m$^2$ planar area associated with live coral and dead coral at the four sampling locations: Solitary Islands (SI), Elizabeth and Middleton Reefs (EMR), Whitsundays (Whit), and Lizard Island (LI). Error indicates standard deviation.

### 4.5.2 Assemblage size spectra

The epifaunal size spectra slopes were also significantly different between live and dead corals (PERMANOVA; density: $df$ = 1, 38, Pseudo-$F$ = 21.4, $P$ <0.001; biomass: $df$ = 1, 38, Pseudo-$F$ = 14.7, $P$ <0.001; productivity: $df$ = 1, 38, Pseudo-$F$ = 29.8, $P$ <0.001). The two density size spectra both had negative slopes, indicating higher densities of smaller animals within assemblages (Fig. 4.3). However, densities on dead corals showed a much steeper slope than on live coral (Fig. 4.3), indicating the dominance of small animals and increasingly similar densities of larger individuals. $R^2$ values suggest dead coral density and productivity size spectra were more consistent than the live coral equivalents, while the live coral biomass size spectrum was more consistent among samples than the dead coral equivalent (Fig. 4.3).

Epifaunal biomass and productivity were also consistently higher on dead coral than on live coral. However, in contrast to densities, trends in biomass and productivity across size spectra were either not as pronounced (dead coral) or reversed, i.e. positive (live coral). The invertebrate body size distribution on dead coral was relatively flat for biomass and negative for productivity. Both biomass and productivity showed a positive trend across size spectra on live coral. Again, these results indicated that the higher productivity of dead coral-associated epifauna was largely driven by the smallest size classes.

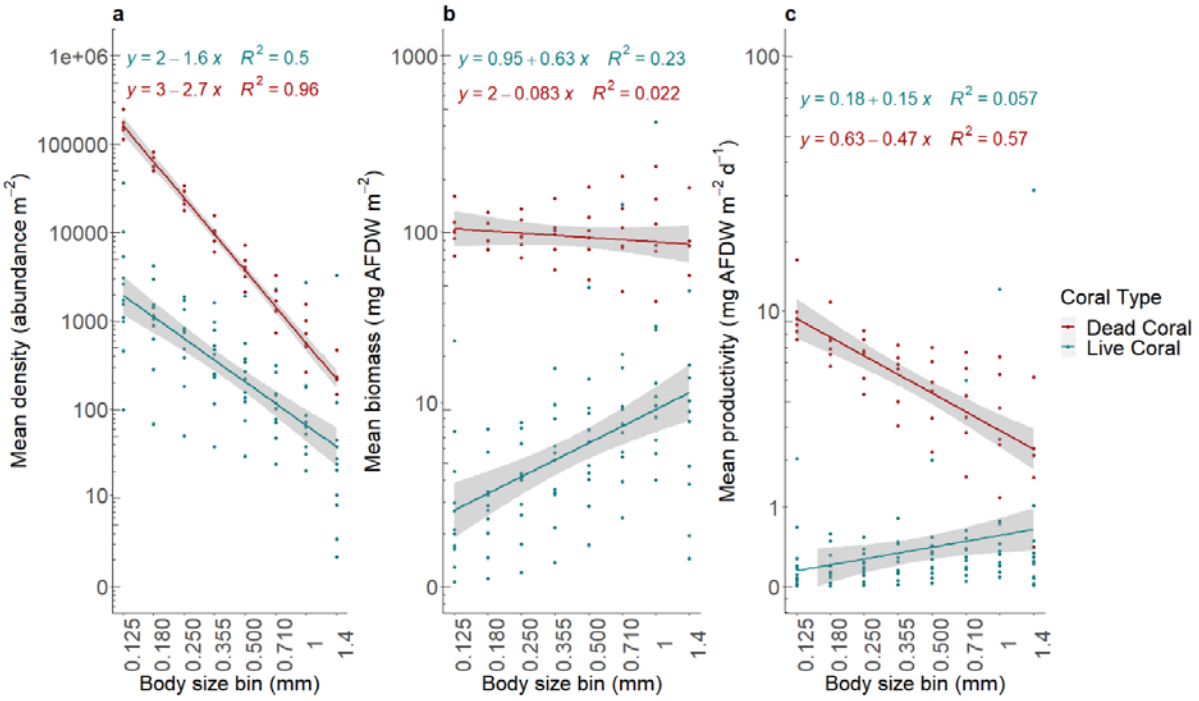


**Fig. 4.3** Contribution of epifaunal invertebrates across size spectra: **(a)** overall assemblage density (abundance $m^{-2}$), **(b)** estimated biomass (mg AFDW $m^{-2}$), and **(c)** estimated daily productivity (mg AFDW $m^{-2}$ $d^{-1}$) in association with live coral and dead coral. Grey shading represents 95% confidence intervals; dots represent sample data within each size bin.

### 4.5.3 Taxonomic composition

Epifaunal assemblages associated with live and dead coral were further analysed for the relative contribution of major invertebrate taxa to overall density, estimated biomass and estimated productivity. Pairwise PERMANOVA indicated that live and dead coral supported distinct epifaunal assemblages (PERMANOVA; density: $df$ = 1/38, $t$ = 2.7, $P$ <0.001; biomass: $df$ = 1/38, $t$ = 2.4, $P$ <0.01; productivity: $df$ = 1/38, $t$ = 2.6, $P$ <0.001).

On both live and dead coral, harpacticoid copepods comprised most invertebrate individuals (Fig. 4.4). By contrast, decapods occurred at low densities, but dominated biomass estimates in both live and dead coral (Fig. 4.4). Decapods also contributed most productivity to live

coral-associated assemblages, but harpacticoid copepods were most important for productivity in dead coral assemblages (Fig. 4.4).

Harpacticoid copepods were more abundant on dead than on live coral and accounted for 80% of the dissimilarity in epifaunal density between live and dead coral (Table 4.4). Differences in epifaunal biomass between live and dead coral were primarily driven by harpacticoid copepods, amphipods, tanaids, ostracods, and isopods, which together accounted for 74% of dissimilarity (Table 4.4). In terms of daily productivity, harpacticoid copepods, amphipods, tanaids, and ostracods together accounted for 77% of dissimilarity between live and dead coral (Table 4.4).

**Table 4.4** Results of SIMPER analysis showing epifaunal taxa (by order-level identification) contributing to 70% of dissimilarity between samples of live and dead coral. Density values are expressed as abundance m-$^{-2}$, biomass as mg AFDW m$^{-2}$, productivity as mg AFDW m$^{-2}$ d$^{-1}$.

| | **Live coral** | **Dead coral** | | | | |
|---|---|---|---|---|---|---|
| **Taxa** | Average values | Average values | Average dissimilarity | Dissimilarity/ SD | Contribution (%) | Cumulative (%) |
| | | | **Density** | | | |
| **Harpacticoida** | 11692 | 231906 | 73.55 | 4.41 | 80.41 | 80.41 |
| | | | **Biomass** | | | |
| **Harpacticoida** | 19.46 | 387.65 | 36.76 | 2.08 | 40.60 | 40.60 |
| **Amphipoda** | 10.02 | 123.78 | 11.31 | 1.40 | 12.49 | 53.09 |
| **Tanaidacea** | 1.39 | 132.51 | 8.74 | 1.05 | 9.65 | 62.74 |
| **Ostracoda** | 0.52 | 66.42 | 6.25 | 1.60 | 6.90 | 69.65 |

| | | | | | | |
|---|---|---|---|---|---|---|
| **Isopoda** | 0.59 | 44.05 | 4.31 | 1.11 | 4.76 | 74.41 |
| | | | **Productivity** | | | |
| **Harpacticoida** | 1.32 | 27.79 | 47.88 | 2.58 | 52.59 | 52.59 |
| **Amphipoda** | 0.28 | 4.66 | 7.88 | 1.24 | 8.65 | 61.24 |
| **Tanaidacea** | 0.06 | 6.25 | 7.40 | 0.95 | 8.13 | 69.37 |
| **Ostracoda** | 0.04 | 4.35 | 7.09 | 1.94 | 7.78 | 77.15 |

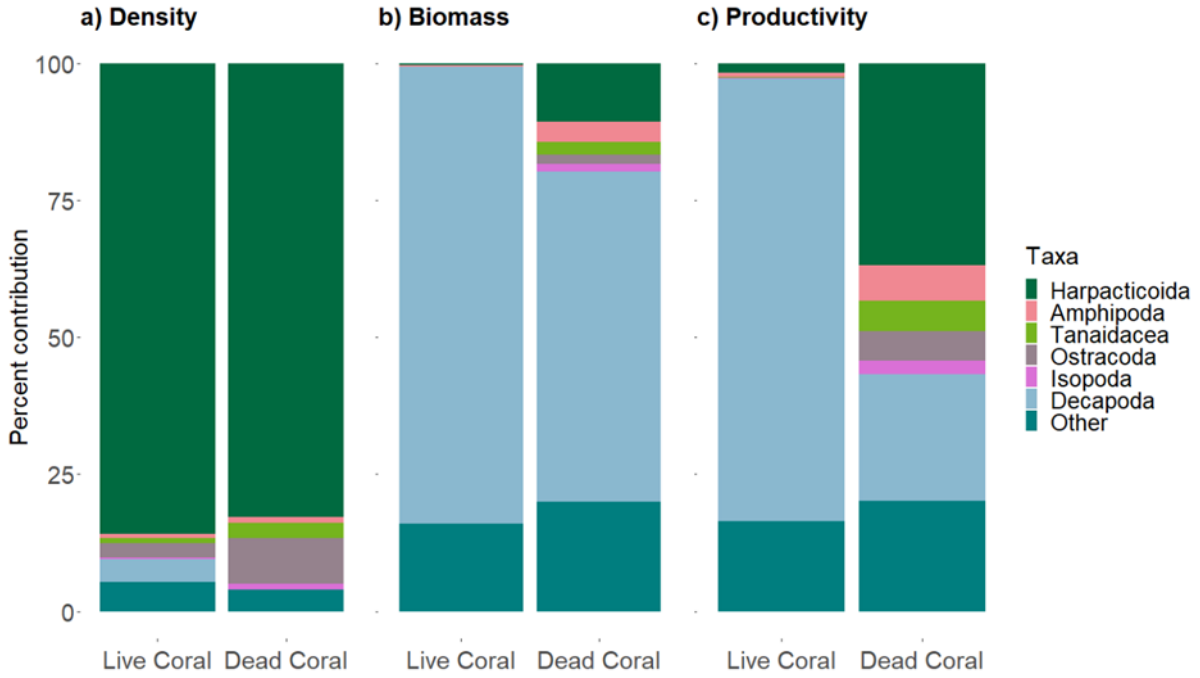


**Fig. 4.4** Percent contribution to **(a)** overall epifaunal density (abundance $m^{-2}$), **(b)** estimated biomass (mg AFDW $m^{-2}$), and **(c)** estimated daily productivity (mg AFDW $m^{-2}$ $d^{-1}$) of the taxa identified by SIMPER analysis as most influential to dissimilarity between live- and dead coral-associated assemblages. Data showing the contribution of decapods are included given their importance to biomass and productivity. Additional taxa grouped as 'other' comprise: Anthozoa, Bivalvia, Chitonida, Gastropoda, Holothuroidea, Mysida, Nematoda, Nemertea, Ophiuroidea, Platyhelmithes, Polychaeta, Pycnogonida, Sabellida, Terebellida.

## 4.6 Discussion

Epifaunal assemblages differed markedly between samples of live and dead coral, with dead coral hosting 1–2 orders of magnitude more epifauna when quantified in terms of overall density, biomass, or productivity. For dead coral-associated assemblages, biomass and productivity size spectra were distinctly flatter than the corresponding density size spectrum. This result is consistent with metabolic theory, whereby much of the energy available to small animals is lost due to metabolic and ecological inefficiencies with each step up the food chain into larger size classes, while turnover rate is slower for larger animals (Sheldon et al. 1972, Sprules and Barth 2016). Epifaunal assemblages, however, cannot necessarily be represented by a simple food chain in which larger epifauna consume their smaller counterparts. While a large proportion of epifaunal taxa are herbivores, depending on microphytobenthos as a food resource (Edgar 1993), small invertebrates on coral reefs represent a wide range of trophic groups, including predatory or opportunistic carnivores, detritivores, filter-feeders (Glynn and Enochs 2011, Poore et al. 2012, Kolasinski et al. 2016) and obligate coral-associates that consume live coral mucus or particles trapped by coral polyps (Galil 1987, Stella et al. 2011). Hence, the relatively shallow slopes of biomass and productivity size spectra may be driven by turnover rate relative to body size, under an assumption that absolute consumption per size class is relatively stable, with more small animals consuming comparable amounts of a food resource to fewer large animals.

In contrast, biomass and productivity in live coral assemblages were higher among larger size classes, and a considerably smaller contribution was made by smaller epifauna to overall density, biomass, and productivity than in assemblages associated with dead coral. This may be explained by the reduced availability of microphytobenthic and detrital food sources on live corals , resulting in less food available for small herbivorous and detritivorous epifauna (Edgar 1993, Poore et al. 2012). Some larger decapod crustaceans rely on basal food sources

directly associated with live coral, such as coral mucus or particles trapped by coral polyps (Galil 1987, Stella et al. 2011, Stella et al. 2014). Predation may also influence size structure, for example, the relative paucity of smaller epifauna, predominantly harpacticoid copepods, on live coral may be related to consumption of very small invertebrates by coral polyps (Goreau et al. 1971, Gochfeld 2004, Houlbréque and Ferrier-Pagés 2009).

Moreover, structure and shelter are key physical components of coral reef ecosystems, with the size of available shelter or refugia correlating with the size structure of associated fauna (Klumpp et al. 1988, Moran and Reaka 1988, Rogers et al. 2014). The structure of live branching coral may be harder for invertivorous fishes – a prolific trophic group on coral reefs (Williams and Hatcher 1983) – to penetrate in order to extract prey, particularly compared with coral rubble (Hixon and Jones 2005). Hence, live branching coral may serve as prey refugia for larger decapods, making live coral habitats favourable to these particular taxa and size classes of invertebrates (Rogers et al. 2014).

Abundance of turfing algae has been shown to relate to the abundance of epifaunal invertebrates on coral reefs more closely than the structural complexity of coral substratum (Klumpp et al. 1988). This may be explained in part by the increased availability of detrital and algal food sources in turfing algae habitat, but turfing algae may also provide substantial shelter for small invertebrates from visual predators and environmental stress (Klumpp et al. 1988).

The lack of clear differences associated with the four reef locations aligned with results of previous research investigating small invertebrates associated with one species of live coral across spatial scales and environmental gradients (Counsell et al. 2018). Variation in assemblage abundance and species richness was greatest at the scale of the individual coral colony and lowest among sites (Counsell et al. 2018). Similarly, an associated study

comparing the taxonomic composition of epifaunal assemblages among diverse benthic microhabitats (e.g. taxonomically and morphologically distinct algal, sponge, and coral microhabitats) on temperate to tropical reefs found strong correlations with habitat structure, largely independent of sampling location (Fraser et al. 2020a) (Chapter 2).

### 4.6.1 Secondary productivity on changing reefs

The notable difference in secondary productivity of small motile invertebrates between live and dead coral samples is relevant to predictions of ecological changes with accelerating climate change impacts. Secondary productivity of motile epifauna in coral reef ecosystems may increase with further loss of live coral, with a shift from larger decapods to small harpacticoid copepods. This shift will affect the flow of energy in reef food webs and the structure of other faunal communities directly and indirectly. Biomass of benthic invertivores and richness of small cryptobenthic fish have been shown to increase following heatwaves and coral bleaching (Stuart-Smith et al. 2018), with these changes potentially influenced by an increase in secondary productivity and availability of smaller prey. Thus, an increase in dead coral habitat within reef systems has the potential to substantially shift the amount of energy available in basal levels of reef food webs.

Thus, the effects of coral mortality on reef food webs are likely to involve complex interactions involving changing food resources, habitat structure and temperature. While live coral loss may lead to higher availability of food for small fishes, degradation of reef structural complexity, most notably the loss of small refugia in the reef matrix, can potentially expose small fishes to increased predation risk (Nash et al. 2013). Habitat structural complexity has been positively correlated with density, biomass and productivity of epifauna (Edgar 1990a, Edgar et al. 1994, Taylor 1998, Kramer et al. 2014, Kramer et al. 2017). Following coral death, coral skeletons become overgrown with turfing algae, then

break down into turf-covered rubble, and eventually degrade further into gravel and sand (Moran and Reaka 1988).

The structural complexity of turf-covered erect coral skeletons and coral rubble sampled here is probably even higher than that of branching live coral habitats at the tiny scales to which small epifaunal invertebrates respond (Kramer et al. 2014). Sand, however, has much less structural complexity for small epifauna, and supports invertebrate communities with generally lower density, biomass and productivity (Kramer et al. 2014, Nelson et al. 2016). Over time, and without recovery of live corals, the secondary productivity supporting critical functions on healthy reefs may therefore be lost resulting in declines in species dependant on this food source and associated effects throughout reef food webs (Enochs and Manzello 2012, Kramer et al. 2015). When invertebrate productivity is considered in the present study, the benefits of increased resources (i.e. epifaunal productivity) appear to exceed the costs of decline in refugia within the reef matrix, and invertivorous fish biomass throughout reef food webs may be maintained or increase (Rogers et al. 2018a). If reefs continue to erode, structural complexity will be lost at scales providing refugia for both small epifaunal prey and larger invertivores, likely leading to declines in biomass and productivity throughout reef food webs (Rogers et al. 2018b).

The differences observed in epifaunal assemblages associated with live coral and turf-covered dead coral suggest increased secondary productivity is initially likely with widespread loss of live coral. This shift is likely to enhance resource availability for benthic invertivores, particularly those specialising on small harpacticoid copepod prey. The consequences of live coral loss, however, can be expected to accentuate over time, as dead corals progressively degrade towards structurally simple sand habitats (Enochs and Manzello 2012). Similarly, effects of live coral loss on fish productivity will reflect trade-offs between potential increases in epifaunal prey availability and progressive decline in structural

complexity (Rogers et al. 2014). Critically, the spatial scale over which coral loss occurs will play a key role in determining the cascading impact of live coral loss on trophic dynamics of reef ecosystems.

## 4.7 Acknowledgements

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# PRODUCTION OF MOBILE INVERTEBRATE COMMUNITIES ON SHALLOW REEFS FROM TEMPERATE TO TROPICAL SEAS

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**Preface:**

*This work has been accepted for publication in a refereed journal and is presented below in identical form. The citation for the paper in press with Proceedings of the Royal Society B: Biological Sciences is:*

Fraser KM, Lefcheck JS, Ling SD, Mellin C, Stuart-Smith RD, Edgar GJ (*in press*) Production of mobile invertebrate communities on shallow reefs from temperate to tropical seas

In Chapter 5 I assess the influence of potential environmental and ecological processes on the daily productivity provided by epifaunal assemblages to reef food webs. Chapters 2 and 3 establish strong habitat associations in terms of the composition and size structure of assemblages. Chapter 5 builds on this information to show how the overall productivity of assemblages vary among habitats, while remaining consistent across the latitudinal gradient. Chapter 5 builds on Chapter 4 by providing a more comprehensive analysis of productivity among habitats, where Chapter 4 indicated clear differences between live coral and turf-covered dead coral habitats.

## 4.8 Abstract

Primary productivity of marine ecosystems is largely driven by broad gradients in environmental and ecological properties. In contrast, secondary productivity tends to be more variable, influenced by bottom-up (resource driven) and top-down (predatory) processes, other environmental drivers, and mediation by the physical structure of habitats. Here, we use a continental-scale dataset on small mobile invertebrates ('epifauna'), common on surfaces in all marine ecosystems, to test influences of potential drivers of temperature-standardised secondary production across a large biogeographic range. We found epifaunal production to be remarkably consistent along a temperate to tropical Australian latitudinal gradient of 28.6°, spanning kelp forests to coral reefs (~3500 km). Using a model selection procedure, epifaunal production was primarily related to biogenic habitat group, which explained up to 45% of total variability. Production was otherwise invariant to predictors capturing primary productivity, the local biomass of fishes (proxy for predation pressure), and environmental, geographic, and human impacts. Highly predictable levels of epifaunal productivity associated with distinct habitat groups across continental scales should allow accurate modelling of the contributions of these ubiquitous invertebrates to coastal food webs, thus improving understanding of likely changes to food web structure with ocean warming and other anthropogenic impacts on marine ecosystems.

## 4.9 Keywords

Macrofauna, epifauna, benthic ecosystems, trophic ecology, community ecology

## 4.10 Introduction

The production and transfer of biomass among constituents of an ecosystem is affected by a diversity of processes that differ among scales. At local scales, biotic interactions such as competition (Wilson and Tilman 1993), predation (Baum and Worm 2009) and facilitation or ecological complementarity (as related to local species richness (Cardinale et al. 2012, Duffy et al. 2017)) influence productivity. In contrast, regional patterns in productivity tend to relate to larger-scale variation in primary producer characteristics, temperature and nutrient availability (i.e. 'bottom up' processes; (Hayduk et al. 2019)). Reconciling these varied drivers of community productivity has long been a goal of ecologists, particularly in marine systems (Strong 1992).

In this era of 'big data,' our capacity to simultaneously evaluate a suite of potential influences has yielded novel insights regarding productivity – a fundamental ecosystem property (Lynam et al. 2017). Phytoplankton productivity, for example, can now be readily assessed across large biogeographic scales using remote sensing tools (Prince and Goward 1995, Schaeffer et al. 2008, Boyce et al. 2010). However, secondary productivity—particularly biomass production at the basal consumer level, including many small heterotrophs that funnel energy through the food web—is less easily quantified, with laborious field assessments generally required (Downing and Rigler 1984, Taylor 1998). For this reason, comparisons of secondary productivity across broad biogeographic scales are relatively rare, and generalized ecological and environmental drivers are yet to be identified (but see (Edgar 1993, Patrick et al. 2019)).

Reef ecosystems are among the most productive and diverse on earth. The productivity of reefs is often quantified in terms of fish production (Morais and Bellwood 2020), fisheries yield (Rogers et al. 2018a, Morais et al. 2020), or the primary productivity generated by

phytoplankton or benthic algae (Miller et al. 2011). A substantial proportion of reef secondary production, though, is generated by small mobile invertebrates ('epifauna') that inhabit the surfaces of macroalgae, coral, and other benthic structures (Edgar and Moore 1986, Taylor 1998). Epifauna are highly abundant, diverse and ubiquitous on shallow reefs worldwide, and represent the main trophic link between benthic primary producers and small carnivores (Holbrook et al. 1990, Kramer et al. 2013). Despite their fundamental role in coastal food webs, the drivers of epifaunal productivity—and thus, 'fuel' for most coastal food webs—have rarely been examined outside highly-controlled experiments (Edgar and Aoki 1993, Duffy et al. 2001) and a few local- to regional-scale investigations (Edgar 1993, Cowles et al. 2009, Hayduk et al. 2019).

Potential drivers of epifaunal productivity can be hypothesized based on documented patterns in other trophic groups and ecosystems, and on relationships described in previous studies of epifauna. Many biological processes are heavily influenced by temperature, and therefore strong latitudinal patterns in productivity are often reported. For example, in forests (Gillman et al. 2015), open oceans (Petersen and Curtis 1980), freshwater streams (Patrick et al. 2019), and seagrass beds (Duarte and Chiscano 1999), productivity is generally highest at equatorial latitudes and lowest towards the poles, largely as a product of metabolic and growth rates scaling with temperature and light (Clarke 2006). Concurrent spatial variation may also suggest unmeasured environmental factors, perhaps including evolutionary processes playing out over longer timeframes that favour more productive traits at low latitudes (Brandt 2000, Myers and Lowry 2009). Moreover, epifaunal secondary productivity may not respond as consistently as primary productivity to latitudinal temperature gradients. Although tropical/temperate differences have been observed (Kramer et al. 2017), previous research indicates there may be no clear pattern in epifaunal productivity across smaller gradients or distinct locations (Virnstein et al. 1984, Edgar 1993).

Both biotic (ecological) interactions and environmental drivers are fundamental determinants of food web structure and function (Conversi et al. 2015), and their relative importance has been debated for several decades (Power 1992, Strong 1992). Local-scale biotic interactions such as predation are clearly important in marine food webs (Paine 1966, Edgar and Aoki 1993, Baum and Worm 2009, Poore et al. 2012), and as such, variation in epifaunal productivity has often been discussed in terms of predation pressure (Edgar 1983, Orth 1992, Kramer et al. 2016). Relationships between epifauna and various metrics of predation pressure, however, are inconsistent (Edgar and Aoki 1993, Chen et al. 2020). Predation effects are further complicated by mesopredator release (Duffy 2006) and the fact that functional groups in addition to obligate invertivores, such as scraping and browsing herbivores, may ingest and assimilate epifauna (Choat et al. 2002, Clements et al. 2016), leading to greater trophic transfer along unexpected pathways. The relationship between secondary productivity and biomass of potential predators may therefore vary along large-scale gradients due to both the functional composition of predator communities and the feeding behaviour within functional groups (Floeter et al. 2004).

In concert with local-scale ecological interactions, broad-scale environmental drivers such as changes in resource supply can equally influence secondary productivity. This phenomenon may play out through changes in the abundance and composition of primary producers , which often correlate with changes in environmental conditions, for example light (moderated by factors such as depth and turbidity in marine ecosystems; (Edgar 1991, 1993)) and nutrient availability (McClanahan et al. 2002b). Previous studies have indicated that food resources appear to set the ceiling on total production of epifaunal communities after accounting for metabolic contributions, with individuals redistributing along a size gradient to maximize community productivity depending on whether they are exposed to predators (Edgar and Aoki 1993).

Local-scale environmental drivers may also affect secondary productivity, albeit often via interactions with local ecological processes or broad-scale environmental drivers. More complex, stable and/or diverse habitats may support higher faunal productivity through provision of greater abundance and diversity of food resources (Taylor 1998, Enochs et al. 2011, Alsterberg et al. 2017, Patrick et al. 2019), thus reducing competition among secondary producers, or through increased protection from predation (Grabowski et al. 2008). Herbivorous amphipods often select more finely complex algal habitat based on the quality of predation refugia, rather than the nutritional quality of the algae (Lasley-Rasher et al. 2011). In addition, while some algal species use chemical defences against fish herbivory, epifauna may be less sensitive to these defences, selecting better-defended algal habitats as a refuge against consumption by omnivores or herbivores (Hay et al. 1988). Local-scale physical conditions – such as wave energy and current flow in marine systems (Hall et al. 2018, Whippo et al. 2018) – and nutrients (McClanahan et al. 2002a) or pollutants (Ling et al. 2018b), can all have substantial effects on faunal community structure and function. These factors, and others such as removal of top predators (Ling et al. 2009, Cinner et al. 2013, Lynam et al. 2017), are often related to proximity and density of human populations (Fowles et al. 2018), and nearby industrial or agricultural activities (Oh et al. 2015, Voss and Bernhardt 2017).

Here, we assembled a continental-scale dataset of shallow reef epifauna consistently surveyed along the east coast of Australia, with the overarching aim of identifying major drivers of variation in epifaunal secondary productivity across biogeographic provinces. Using multi-model inference, we tested six hypotheses relating to expectations from ecological theory and prior evidence (Table 5.1). We hypothesized that, like primary production, the major constraints on local secondary production across large scales would be set by the amount of resources and the abiotic environment, with smaller roles for biotic and other factors.

## 4.11 Materials and methods

### 4.11.1 Study area and field sampling

Epifauna were sampled on shallow reefs at 11 eastern Australian locations, from southern Tasmania (43.3°S) to Lizard Island in the northern Great Barrier Reef (14.7°S) (Fig. 5.1). Within this study area, temperate waters south of 30°S can be separated into cool temperate and warm temperate. Cool temperate waters (Southern Tasmania, Eastern Tasmania, Kent Group), support rocky reefs with more canopy-forming macroalgae and an overall richer algal flora than warm temperate reefs (Eden, Jervis Bay, Sydney, Port Stephens) (Sanderson 1997). Subtropical reefs in the region of approximately 30°S may be rock- (Solitary Islands) or coral-based (Elizabeth and Middleton reefs), with subtropical rocky reefs colonised by a combination of macroalgae and coral veneer (Dalton and Roff 2013). Tropical reefs north of approximately 30°S are dominated by corals (Whitsundays, Lizard Island) (Hughes et al. 1999).

A total of 132 samples of diverse benthic microhabitats (comprising the most common biogenic microhabitats available on rocky and coral reefs) and associated epifaunal invertebrates were collected via SCUBA. Site selection, and sample collection and preservation follow protocols described by Fraser et al. (2020a) (Chapter 2). At each location, between 3 and 11 sites were sampled (mean = 5 sites) (Fig. 5.1). At each site, between 2 and 9 samples were collected (mean = 6 samples) across the range of available microhabitats. Sampling depths ranged from 1 – 14 m (mean = 4.5 m), depending on the depth of accessible reef; microhabitats were sampled randomly across this depth range. Within locations, sites were separated by at least 2.5 km. Microhabitat samples were enclosed within 22 x 22 cm plastic bags and removed with a knife (algae, soft coral, and sponges) or chisel (branching coral). Epifauna on microhabitats that could not easily be removed (turfing algae and massive

corals) were collected using a venturi suction sampler with animals retained in a 0.5 mm mesh bag. Live coral samples were washed three times in fresh water to remove epifauna, which were then fixed in a 5% buffered formalin solution; all other samples were fixed immediately in a 5% buffered formalin solution (Fraser et al. 2020a) (Chapter 2).

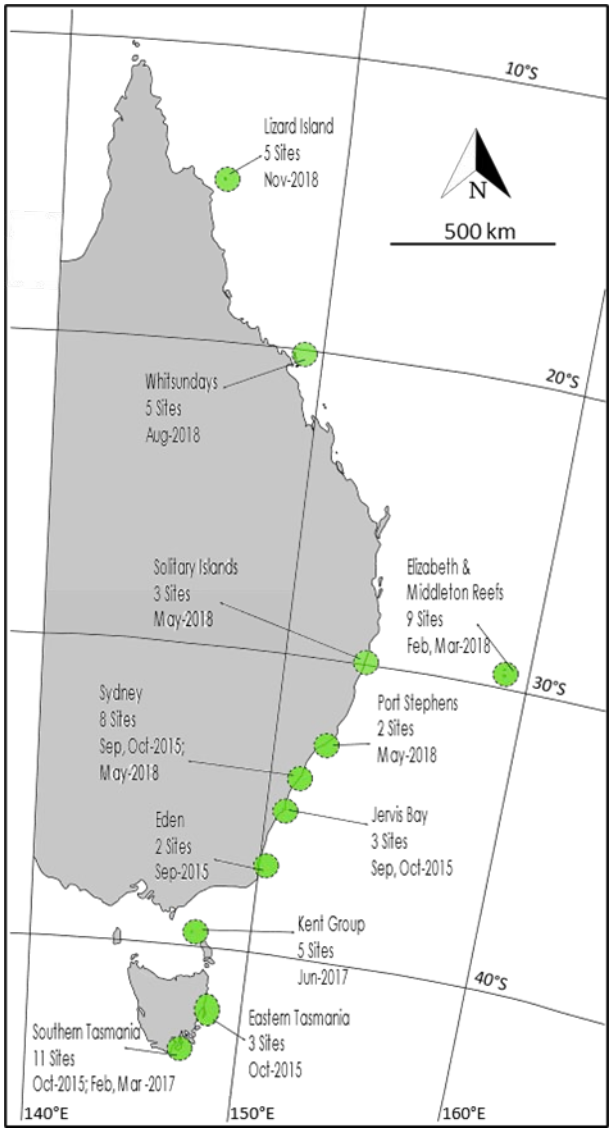



**Fig. 5.1** Map of eastern Australia showing sampling locations, sampling dates and number of sites.

### 4.11.2 Laboratory processing and description of variables

#### *4.11.2.1 Productivity estimates*

Preserved invertebrates from each sample were passed through a nested series of 12 sieves stacked in descending order of mesh size, following a $\log_{\sqrt{2}}$ series (8, 5.6, 4.0, 2.8, 2.0, 1.4, 1.0, 0.71, 0.5, 0.355, 0.25, 0.18, 0.125 mm, after Edgar (1990b)). Invertebrates retained on each sieve were washed into petri dishes and counted under a dissecting microscope, with data binned by sieve mesh size.

The venturi suction method (Fraser et al. 2020a) (Chapter 2) used to sample microhabitats that could not easily be removed for sampling (i.e. massive corals and turfing algae), resulted in a loss of animals through the mesh bag (<0.5 mm body size). For each of these samples, abundance estimates of smaller animals were extrapolated by taking the slope and intercept of the linear regression ($\log_{10}$ (abundance + 1) against $\log_{10}$ (sieve mesh size)) for mesh sizes 0.5–2 mm. The linear regression slope and intercept were used to estimate $\log_{10}$ (abundance + 1) for each of the sieves with mesh size <0.5 mm; data were then back-transformed to give estimated abundance for each size bin. Prior investigation indicated that extrapolation had high predictive accuracy (Fraser et al. 2020c) (Chapter 3).

Epifaunal abundance data by size bin were standardised to 1 $m^2$ planar seabed area (density) prior to analysis following Fraser et al. (2020a) (Chapter 2). Standardisation by seabed area was considered most appropriate for comparing epifaunal productivity to other trophic groups such as fishes in food web models.

To calculate productivity, epifaunal biomass as ash-free dry weight (AFDW) of individuals within each size bin was first derived from published estimates of mean biomass across macrofaunal taxonomic groups (Edgar 1990b). Productivity estimates were calculated using the general allometric equation given by Edgar (1990b):

$$P = (10\text{^}((-2.31 + 0.8 * \log10(\mathrm{B} * 1000) + 0.89 * \log10\mathrm{T}))/1000$$

where *P* is productivity of an individual (mg AFDW $d^{-1}$), *B* is the biomass of an individual (mg AFDW), and *T* is water temperature (°C) at the time of sampling. Productivity estimates of individual animals were then multiplied by density within each size bin, and size bin productivity estimates summed to provide total productivity estimates (mg AFDW $m^{-2}$ $d^{-1}$) for each sample. Productivity was calculated for a standardised temperature of 20°C following Edgar (1993), and hereafter referred to as $P_{20}$. The use of $P_{20}$ is recommended to eliminate the effects of temperature when investigating food webs, assuming that metabolic and growth rates respond similarly to temperature change across trophic levels (Edgar 1993). We note that this method for estimating biomass and productivity was originally established for individuals ≥0.5 mm; here we assume the equations used by Edgar (1990b) also apply to smaller individuals (≥0.125 mm) based on linear extrapolation of well-supported trends (i.e. $R^2$ ranging from 0.87 to 0.98 (Fraser et al. 2020c) (Chapter 3)).

In order to visualize variation in epifaunal productivity across the latitudinal gradient while accounting for microhabitat variation among sampling locations, the fraction of benthic cover provided by each microhabitat within each site was multiplied by the epifaunal productivity associated with that microhabitat to give estimated productivity per $m^2$ of seabed ('site productivity'). To estimate the proportional cover of microhabitats within sites, 20 benthic 'photo quadrats' were taken along a 50 m transect set through the site, which were later visually assessed (see the Reef Life Survey methods manual for further detail: https://reeflifesurvey.com/methods/; see Fraser et al. (2020c) (Chapter 3) for details of matching benthic cover data to epifaunal data).

*4.11.2.2 Predictor variables*

Predictor variables and the models in which they are applied are summarised in Table 5.1, while details of predictor variables are provided in Appendix (Table 5.2)

Total fish biomass and cryptic fish abundance data were extracted from the Reef Life Survey database (RLS; http://reeflifesurvey.com/; (Edgar and Stuart-Smith 2014)) and the Long-term Australian Temperate Reef Collaboration database (ATRC; http://atrc.org.au/). Visual census data were collected from 50 m-long (RLS) or 100 m-long surveys (ATRC) at the same sites as epifaunal sampling (i.e. within ca. 50 m). Surveys involved counting and identifying all mobile reef-associated fishes (excluding cryptic fishes) in 5 m belts either side of a transect line and placing counts in estimated size bins. All cryptic fishes were counted, identified, and assigned to size bins from a 1 m belt either side of a transect line. Visual census dates coincided with epifaunal sampling dates, otherwise fish data were used from the closest available date.

Biomass of all reef-associated fishes (excluding planktivores and cryptic fishes) was calculated using fish length and abundance data and species-specific length-weight coefficients obtained from FishBase (2019), as in previous studies (Edgar and Stuart-Smith 2009, Stuart-Smith et al. 2018). Cryptic fishes were classified as inconspicuous fishes closely associated with the bottom, usually small but including some large-bodied fishes such as moray eels, and belonging to a defined set of families, as listed in the Reef Life Survey methods manual (available at https://reeflifesurvey.com/methods/).

Environmental data (sea surface temperature, chlorophyll-a) were obtained from Bio-ORACLE (Tyberghein et al. 2012), matched to sampling sites. The index of human population pressure (as used in previous studies, e.g. (Edgar et al. 2014)) was calculated by fitting a smoothly curved surface to each settlement point on a year 2015 world population

density grid using the quadratic kernel function. The population grid was obtained from the Gridded Population of the World Version 4 (GPWv4): Population Grids (CIESIN et al. 2005). For each site, we also applied a four-level categorical measure for wave exposure: (1) sheltered, with only wind waves from non-prevailing direction, (2) wind-generated waves from the prevailing direction, (3) exposed to ocean swells, either indirectly with exposure to prevailing winds, or directly but sheltered from prevailing winds, or (4) exposed to open ocean swell from prevailing direction. Similar categorical assessments were made at each reef site of the vertical relief of the reef, the angle of reef slope and exposure to currents, with a score of 1 representing the flattest reefs not exposed to currents and with 4 assigned to highly complex structure, steep slopes or severe currents.

Sampled microhabitats were categorised using the CATAMI scheme (Althaus et al. 2015), which combines taxonomy and morphology as a national standard for Australian benthic microhabitat classification. Microhabitats were further aggregated into four major habitat groups: macroalgae, live coral, sessile invertebrates (soft coral and sponges), and turfing algae (Fraser et al. 2020c) (Chapter 3). Structural characteristics of sampled microhabitats were assessed based on characteristics identified by Edgar (1994) and Fraser et al. (2020a) as important for epifaunal community structure: degree of branching (complexity metric following (Edgar 1983); order of the primary axis, whenever an axis splits the order increases by one); maximum length (length of sampled microhabitat from base to distal tip) (see Appendix (Table 5.2) for further detail of predictor variables).

### 4.11.3 Data analyses

Estimated epifaunal $P_{20}$ per $m^2$ of seabed (estimated by multiplying the fraction of benthic cover provided by each microhabitat within each site by the estimated $P_{20}$ associated with that microhabitat) was averaged within each of the 11 sampling locations to give mean $P_{20}$ (mg

AFDW $m^{-2}$ $d^{-1}$) for each location. These data were plotted against latitude using a linear model in R (R Development Team 2017).

Six hypotheses were tested using multiple regression models parameterised with the appropriate predictors (Table 5.1) in a multi-model inference framework (Burnham and Anderson 2002) (see (Fraser et al. 2020b) for the dataset and R code used for analysis). We fit a separate linear model to $\log_{10}$ transformed $P_{20}$ (per $m^2$ of individual microhabitat sampled) to test each hypothesis with the set of associated predictor variables using the full (not summarized per location) dataset ($n$ = 115) (Table 5.1). Assumptions of each model were tested using variance inflation factors (VIF) for independence of predictors and residuals examined to ensure normality. We then used Akaike information criterion with small sample correction (AICc) to evaluate the likelihood of each model. We selected the best-supported model based on the Akaike weight, which describes the relative likelihood of each model given the candidate set of models. The Akaike weight (AICwt) ranges from 0-1, with 0 being no support and 1 being total support (Burnham and Anderson 2002). The best supported models were further evaluated by Type-III ANOVA using the *car* package (Fox and Weisberg 2019) and Tukey post-hoc comparison of means. We fit the models using R version 3.6.3 (R Development Team 2017) and used the *AICcmodavg* package to compute Akaike weights (Mazerolle 2019).

Analyses described above were also conducted using temperature-dependent productivity (results presented in Table 5.3 (S1)). However, since modelling temperature-dependent productivity as a function of temperature could lead to mathematical dependence between the response and the predictor, $P_{20}$ was chosen as the preferred response variable.

## 4.12 Results

Across 28.6 degrees of latitude, we found little variation in total epifaunal community productivity ($P_{20}$; mg AFDW $m^{-2}$ $d^{-1}$), at both the individual sample level and the location level based on the contribution of different microhabitats to total benthic cover (Fig. 5.2a). The lack of variation in productivity standardized by temperature ($P_{20}$) with latitude indicates that epifaunal productivity should maintain similar productivity relativities with other food web elements (e.g. fishes, primary producers), all equally varying with temperature as predicted by metabolic theory.

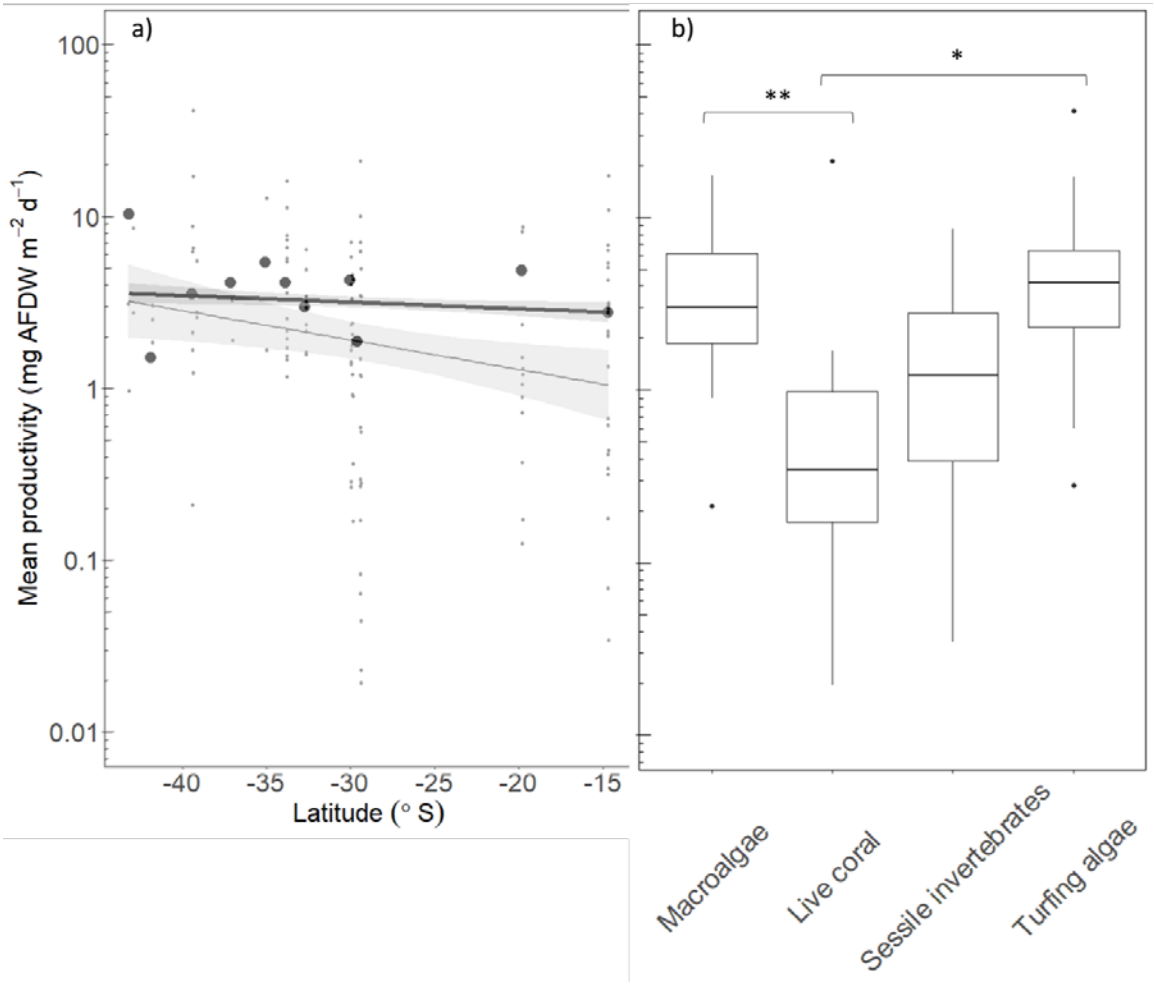



**Fig. 5.2** Linear regression **(a)** of mean $\log_{10}$ total epifaunal community daily productivity ($P_{20}$) against latitude. The large black points represent mean $P_{20}$ within each of the 11 sampling locations, estimated by multiplying the fraction of benthic cover provided by each

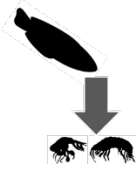
microhabitat within each site by the estimated $P_{20}$ associated with that microhabitat; the black line represents the regression of those data against latitude. The small grey points represent epifaunal $P_{20}$ for individual samples; the grey line represents the regression of those data against latitude. Grey shading represents 95% confidence intervals. Box plots **(b)** of variation in $\log_{10}$ epifaunal assemblage $P_{20}$ among habitat groups. Horizontal lines in each box plot represent third quartile, median and first quartile. The whiskers extend to 1.5 x interquartile range. Dots represent outliers. Asterisks indicate significant differences between habitat group pairs (*$P$<0.05; **$P$<0.01).

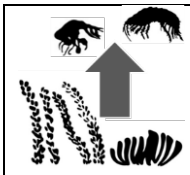
The habitat group model was overwhelmingly the best supported model to explain variation in epifaunal $P_{20}$ (AICwt = 0.96; Table 5.1), suggesting that epifaunal secondary productivity is predominantly driven by characteristics of the immediate habitat group occupied by an assemblage (i.e. macroalgae, live coral, sessile invertebrate, or turfing algae). The microhabitat model, which includes finer but more numerous microhabitat categories than the habitat group model, was supported to a much lesser degree (AICwt = 0.04), suggesting that the explanatory power gained by this increased resolution was not worth the loss of additional degrees of freedom, while all other hypotheses had no support according to their Akaike weights (Table 5.1).

Within the habitat group model, epifaunal $P_{20}$ differed significantly among habitat groups ($F$-value = 19.4, $P$ <0.001; Fig. 5.2b; Table 5.4 (S2)). Tukey pair-wise comparison of mean $P_{20}$ among habitat groups indicated significant differences between macroalgae and live coral ($P$ = 0.0033), and between turfing algae and live coral ($P$ = 0.010). Epifaunal $P_{20}$ also showed a significant positive correlation with branching ($F$-value = 6.3, $P$ = 0.011; Fig. 5.3a; Table 5.4 (S2)). However, the effect of branching varied significantly among habitat groups ($F$-value = 3.3, $P$ = 0.024; Table 5.4 (S2)), with the overall positive correlation between branching and $P_{20}$ largely driven by macroalgae and turfing algae habitat groups (Fig. 5.3a).

Our model selection analysis suggests that the near constant epifaunal productivity observed on reefs along the east coast of Australia is a product of trade-offs in the dominant habitat groups across the latitudinal gradient (Fig. 5.4). Moving from tropical to temperate latitudes, the loss of live coral and associated secondary productivity is compensated by increased contributions by communities of epifauna inhabiting turfing algae and sessile invertebrate habitat groups, while macroalgal communities remain reasonably constant across the entire latitudinal range.

**Table 5.1** The hypotheses (epifaunal community $P_{20}$ is predominantly driven by: H1 – H6) and linear models tested to explain variation in epifaunal $P_{20}$, with predictions (P) included within models. Partial $R^2$ indicates the proportion of variance explained by each predictor within models; multiple $R^2$ indicates the raw unadjusted $R^2$ for each model. Model selection was based on the Akaike weight, which describes the relative likelihood of each model given the set of candidate models.

| **Hypothesis (H)** | **Model and Predictions (P)** | **Partial $R^2$** | **Multiple $R^2$** | **Akaike weight** |
|---|---|---|---|---|
| **H1 –Predation pressure**  | **PREDATION MODEL** | | 0.032 | <0.01 |
| | P1 – $P_{20}$ declines with increased total fish biomass | 0.004 | | |
| | P2 – $P_{20}$ declines with increased cryptic fish abundance | 0.029 | | |
| **H2 – Resource availability** | **RESOURCE MODEL** | | 0.122 | <0.01 |
| | P3 – $P_{20}$ declines as depth increases (reducing light) | 0.031 | | |

| | | | | |
|---|---|---|---|---|
|  | P4 – $P_{20}$ increases with epiphyte load | 0.048 | | |
| | P5 – $P_{20}$ increases with chlorophyll-a | 0.005 | | |
| | P6 – $P_{20}$ increases with mean SST | 0.038 | | |
| **H3a – Characteristics of immediate habitat, fine microhabitat scale**  | **MICROHABITAT MODEL** | | 0.594 | 0.04 |
| | P7 – $P_{20}$ varies significantly among microhabitats | 0.548 | | |
| | P8 – $P_{20}$ increases with habitat branching/complexity | 0.025 | | |
| | P9 – $P_{20}$ increases with the maximum length of habitat | 0.021 | | |
| **H3b – Characteristics of immediate habitat, coarse habitat group scale**  | **HABITAT GROUP MODEL** | | 0.450 | 0.96 |
| | P10 – $P_{20}$ varies significantly among habitat groups | 0.344 | | |
| | P11 – $P_{20}$ increases with habitat branching/complexity | 0.030 | | |
| | P12 – the effect of branching on $P_{20}$ varies among habitat groups | 0.069 | | |
| | P13 – $P_{20}$ increases with the maximum length of habitat | 0.007 | | |
| **H4 – Local environmental factors**  | **ENVIRONMENT MODEL** | | 0.114 | <0.01 |
| | P6 – $P_{20}$ increases with mean SST | 0.049 | | |
| | P14 – $P_{20}$ declines with increased wave exposure | 0.036 | | |
| | P15 – $P_{20}$ declines with increased relief | 0.009 | | |
| | P16 – $P_{20}$ declines with increased slope | 0.014 | | |
| | P17 – $P_{20}$ declines with increased current strength | 0.006 | | |
| **H5 – Geographic location** | **SPATIAL MODEL** | | 0.091 | <0.01 |
| | P18 – $P_{20}$ declines towards higher latitudes | 0.054 | | |

| | | | | |
|---|---|---|---|---|
|  | P19 – $P_{20}$ varies significantly with longitude | 0.037 | | |
| **H6 – Human population impacts**  | **HUMAN IMPACTS MODEL** | | 0.077 | <0.01 |
| | P20 – $P_{20}$ increases with human population density | 0.077 | | |

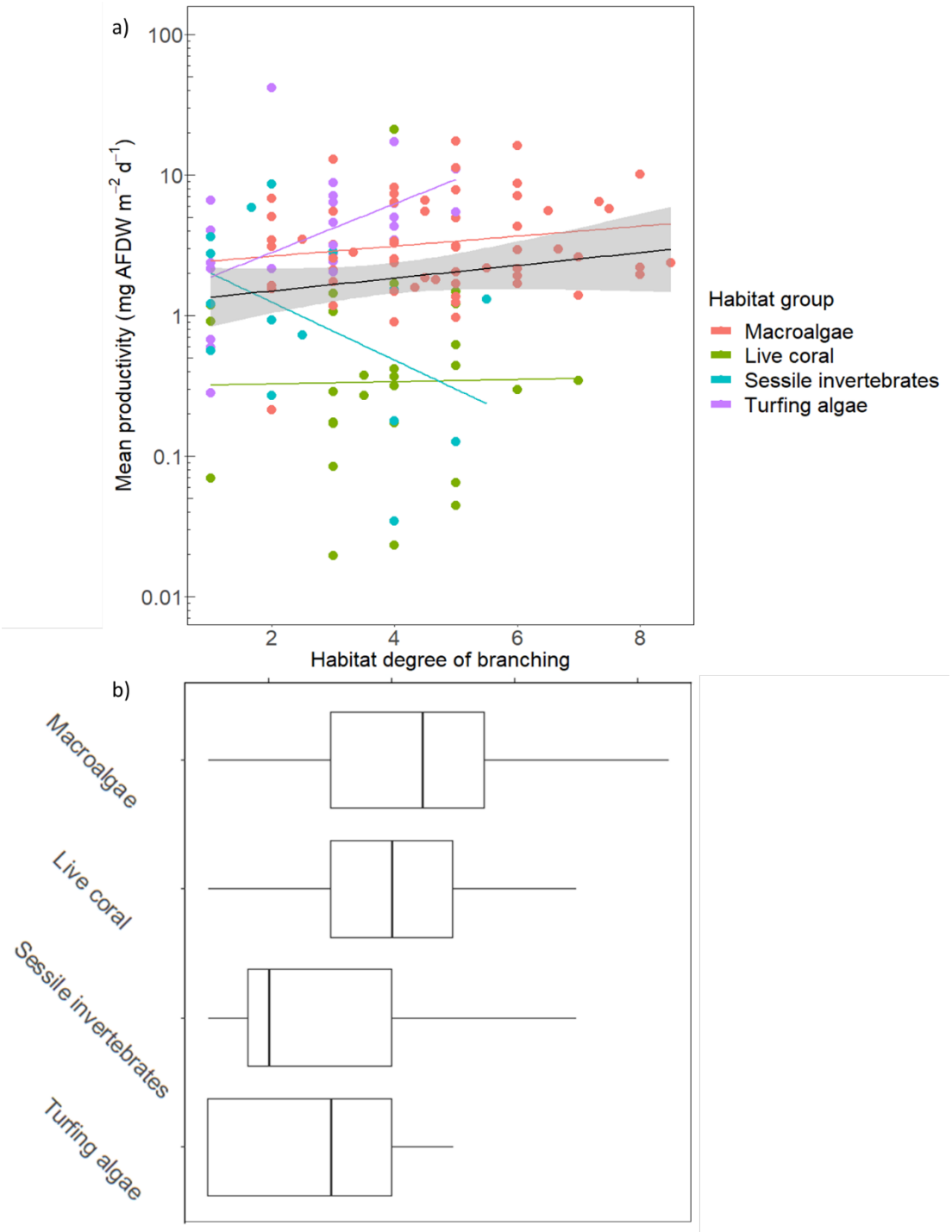



**Fig. 5.3** Linear regression **(a)** of mean $\log_{10}$ epifaunal $P_{20}$ against habitat degree of branching, with colours indicating habitat groups, and black line the overall mean. Higher branching equates to higher complexity and translates to higher productivity on average. Points represent individual samples; grey shading represents 95% confidence interval of overall mean. Horizontal boxplots **(b)** show variation in the degree of branching within each habitat group. Vertical lines in each box plot represent third quartile, median and first quartile. The whiskers extend to 1.5 x interquartile range.

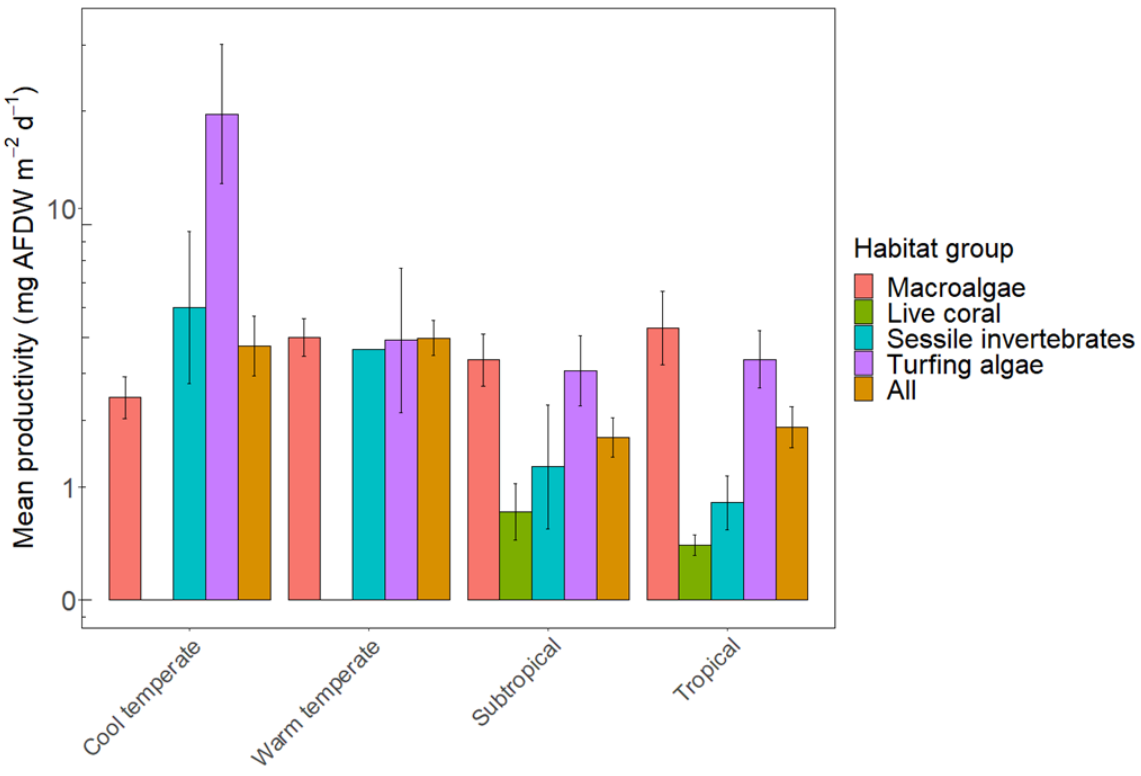



**Fig. 5.4** Mean $\log_{10}$ epifaunal $P_{20}$ associated with each habitat group across four climatic zones within the latitudinal gradient sampled. Mean $P_{20}$ among habitat groups is represented for each climatic zone by the bar titled 'All'. Climatic zones represent the following latitudinal ranges: cool temperate (-43.3 to -37.7°S), warm temperate (-37.6 to -31.9°S), subtropical (-31.8 to -26.1°S), tropical (-20.4 to -14.6°S).

## 4.13 Discussion

Ecosystem productivity has historically been considered to be predominantly a function of environmental drivers that regulate the availability of resources (Strong 1992, Boyce et al. 2015, Lynam et al. 2017). Here, we find that habitat group primarily determines the degree of secondary productivity provided by small marine invertebrates to shallow reef food webs. Trade-offs in the local productivity afforded by each of four broad habitat groups (corals, macro- and turfing algae, and sessile invertebrates) led to a remarkably consistent trend in epifaunal secondary productivity from temperate to tropical zones.

While community structure and function have long been viewed through the lens of resource control, the controlling resource has often been framed in terms of biomass and energy transfer among trophic groups (i.e. carbon acquisition) (Edgar 1993, Worm and Duffy 2003, O'Gorman et al. 2008, Lynam et al. 2017). However, niche theory also acknowledges space as an important resource (i.e. the 'Hutchinsonian' niche), harkening back to seminal contributions on the organization of sessile organisms in rocky intertidal ecology (Connell 1961, Dayton 1971). Habitat resources, additional to food resources, appear responsible for large-scale patterns in epifaunal community structure (Fraser et al. 2020a, Fraser et al. 2020c) (Chapter 2, Chapter 3). This seems also to be the case in the current study with regards to their production, echoing a recent finding in communities of freshwater stream invertebrates in North America (Patrick et al. 2019).

### 4.13.1 Why is habitat so important?

Several potential mechanisms may explain our finding. First, while epifaunal assemblages comprise a diversity of functional groups, herbivores (the 'mesograzers') typically dominate (Hay et al. 1987, Edgar 1993). Mesograzers tend to rely on microphytobenthic films and filaments, with some larger animals consuming macroalgae (Kramer et al. 2012). Macroalgal habitats present abundant food resources in the form of microphytobenthos and host algal tissue, potentially facilitating greater productivity of epifauna than habitats without these resources (Poore et al. 2012). Filamentous turfing algae, in addition to offering a direct food source for mesograzers, tends to host microalgal films and capture high volumes of detritus (Connell et al. 2014), presenting an abundance and diversity of trophic resources for different epifaunal functional groups (Kramer et al. 2012). By contrast, live hard coral offers minimal food for herbivorous mesograzers (Grabowski 2004, Yamashiro et al. 2012), making it largely food resource-poor except for particles trapped by coral polyps and the coral mucus consumed by some larger decapod taxa (Galil 1987). Epifauna selecting soft coral and sponge

habitats, comprising the sessile invertebrate habitat group, are likely to encounter fewer food resources. Soft corals use allelopathic defences to resist colonisation by microphytobenthos and epiphytes, and consumption by epifauna (Coll et al. 1982). Sponge tissue is consumed by some epifauna, however most sponge-dwellers consume external food sources (Oshel and Steele 1985, Poore et al. 2000).

Variation in epifaunal productivity may also be influenced by differential predation susceptibility among benthic habitats. Habitat structural complexity and its role in shaping predator-prey relationships has long been discussed (Crowder and Cooper 1982, Grabowski 2004, Grabowski et al. 2008, Warfe et al. 2008), and may be a factor determining the relationship between epifaunal productivity and habitat groups. Epifaunal productivity increased with our metric of habitat complexity (degree of branching) (Fig. 5.3a), presumably due to the added protection from predators offered by more complex habitat (Orth et al. 1984, Warfe et al. 2008). However, the degree to which this benefit is realized depends greatly on the habitat type (Fig. 5.3a, 5.3b). For example, macroalgal habitat was the most highly branched and supported among the highest estimates of epifaunal productivity, however live coral was also highly branched but supported the least productive epifaunal assemblages.

This apparent inconsistency raises the question of whether physical complexity provides actual or perceived refuges for epifaunal prey (Grabowski 2004), and may be partly resolved by considering the scale at which complexity is quantified. While live branching coral is complex at scales ranging from millimetres to centimetres, the complexity of turfing algae is at a sub-millimetre to millimetre scale, and macroalgae complexity ranges from sub-millimetre through to centimetres (Kramer et al. 2017). In studies comparing macroalgae species (Zamzow et al. 2010) or artificial algal habitats of differing complexity (Klecka and Boukal 2014), small invertebrates generally select more finely complex habitat that offers predation refugia appropriate for the invertebrate body sizes. Macroalgae complexity can also

be finely partitioned by much larger herbivorous fishes (Brandl and Bellwood 2016). If microhabitat complexity were quantified to higher resolution, for example by using fractal dimensions (Gee and Warwick 1994a), stronger relationships between epifaunal productivity and habitat complexity would perhaps be evident, as would consistency between the complexity of habitat groups and the productivity they support.

In addition to complexity, predation pressure may vary as a result of particular characteristics of the different habitat groups. For example, while the heterotrophy of hard corals largely involves the consumption of zooplankton (Goreau et al. 1971, Houlbréque and Ferrier-Pagés 2009), small epifaunal invertebrates could fall prey to coral polyps. Hard corals also often use physical defence strategies, such as 'sweeper tentacles', to resist colonization by small epiphytes and epifauna (Gochfeld 2004). In addition, the rigid structure of branching hard coral limits the ability of mobile invertivores (e.g. fish) to penetrate the habitat in order to extract epifaunal prey (Hixon and Jones 2005). Hence, branching coral can provide refugia for larger epifaunal invertebrates that may be less susceptible to consumption by coral polyps (Kramer et al. 2016, Fraser et al. 2020c, *in review*) (Chapter 3, Chapter 4).

Fish communities on tropical reefs have been shown to comprise proportionally more herbivores compared with temperate reefs, which support more omnivorous fishes, while invertivores are consistently common across all latitudes (Longo et al. 2019). While total fish biomass is used here as a proxy for predation pressure, understanding the differences in predation exposure for epifauna among different microhabitats would require more detailed study of the functional composition and feeding behaviour of local fish communities. For example, predation by omnivores or consumption of epifauna by herbivores may vary among algal microhabitats depending on chemical defences against fish herbivory or the palatability of algae, as epifaunal invertebrates may be insensitive to chemical defences (Hay et al. 1988)

or choose less palatable algal microhabitats based on refuge quality (Lasley-Rasher et al. 2011).

Interestingly, neither site-scale estimates of predator biomass, nor temperature or primary productivity (assessed using water column chlorophyll content as a proxy) appeared to be explicitly related to variation in epifaunal productivity. Our use of $P_{20}$ controls for a major environmental factor, temperature, although theory and recent studies suggest that temperature effects are most likely to manifest through enhancing the (consumable) resource base, rather than acting directly on community production (Brown et al. 2004, Cusson and Bourget 2005, Patrick et al. 2019). Metabolic rate scales with temperature at approximately similar rates across trophic levels, resulting in proportionally similar production/temperature changes (Edgar 1993). Given that habitat group affects potential food resources available for epifauna, whereas temperature had little apparent influence on secondary productivity, our results are consistent with the hypothesis that epifaunal productivity is limited predominantly by food resource ceilings (Edgar 1993, Edgar and Aoki 1993).

### 4.13.2 Ecological implications

Epifaunal invertebrates are extremely prolific in coastal and shallow reef ecosystems, with a very high proportion of their biomass consumed by larger invertebrate predators and fishes (Taylor 1998). Consequently, epifaunal communities comprise a critical basal component in shallow marine food webs (Orth et al. 1984). Understanding the factors that promote productive epifaunal communities is crucial for the goal of ensuring high trophic transfer and food web stability for coastal and shallow reef ecosystems. Given that the biotic habitat group occupied by the epifaunal assemblage was here found to explain >45% of the variance in secondary productivity along an extensive biogeographic gradient, understanding changes to benthic habitat group availability is the critical first step to achieving this goal.

In selecting microhabitats to sample, we attempted to include all common types of biogenic cover found on shallow coral and rocky reefs in eastern Australia. However, direct anthropogenic stressors, combined with climate change, are shifting the distribution and abundance of biogenic habitat groups common to rocky and coral reefs (Filbee-Dexter and Wernberg 2018, Hughes et al. 2018, O'Brien and Scheibling 2018). Our results reveal an important indirect pathway for the effects of global, regional, and local scale environmental changes to alter reef ecosystems. Ocean temperature has been identified as the most important driver of the benthic composition of biogenic habitat groups on both rocky and coral reefs (Cresswell et al. 2017). Other important drivers include human population density, nutrient availability, wave exposure, and the density of habitat-transforming fauna such as herbivorous sea urchins or corallivorous crown-of-thorns sea stars (Ling 2008, De'ath et al. 2012, Cresswell et al. 2017). Turf and sometimes macroalgae are succeeding corals lost to bleaching and other local stressors (Mumby et al. 2007a, Nelson et al. 2016, O'Brien and Scheibling 2018). Macroalgae beds on rocky reefs are declining in many regions (Krumhansl et al. 2016), often to be replaced by turf as oceans warm and voracious herbivores undergo range extensions and population outbreaks (Ling et al. 2015, Filbee-Dexter and Wernberg 2018, Reeves et al. 2018).

Mediated by shifts in available reef habitat groups, these drivers can potentially affect epifaunal invertebrate communities and food web processes. Our results imply changes to epifaunal secondary productivity should be predictable if habitat group transformation is well documented or accurately predicted. Replacement of live coral by turfing algae or macroalgae will likely increase epifaunal secondary productivity on tropical and subtropical reefs (Fig. 5.4) (Fraser et al. *in review*) (Chapter 4). If turf replaces macroalgae on temperate reefs, a significant increase in epifaunal productivity may be expected, whereas the succession of subtropical macroalgae by turf is likely to result in minimal change (Fig. 5.4).

Rather, relatively high epifaunal productivity may be maintained on subtropical reefs, as turfing and macroalgae both support similarly highly productive assemblages of epifaunal invertebrates.

## 4.14 Acknowledgements

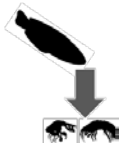
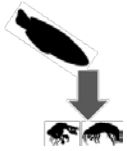
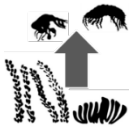
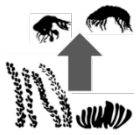
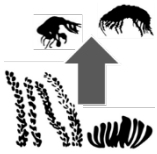
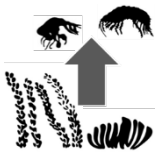
This study was supported by Australian Research Council grants to GJE (LP100200122) and SDL (DP170104668), and an Australian Postgraduate Award to KMF. Fieldwork was additionally supported by the Marine Biodiversity Hub – a collaborative partnership supported through the Australian Government's National Environmental Science Programme, as well as Parks Australia, the Sydney Institute for Marine Science, the Australian Museum's Lizard Island Research Station, and the Ian Potter Foundation. Human population density data were modelled by Stuart Kininmonth.

## 4.15 Appendix

### 4.15.1 Predictor variables

**Table 5.2 (Appendix)** Predictor variables applied in models to test each hypothesis, with units, brief description and data source (concurrent with sample collection or processing ('Sampling'), Reef Life Survey (RLS) (Edgar and Stuart-Smith 2014), Bio-ORACLE (Tyberghein et al. 2012), or the Gridded Population of the World Version 4 (GPWv4) (CIESIN et al. 2005)).

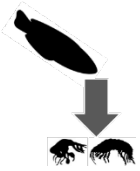
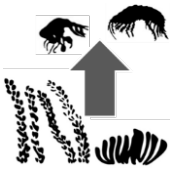
| Hypothesis (H): model name | Predictor variable | Units | Description | Source |
|---|---|---|---|---|

| | | | | |
|---|---|---|---|---|
| H1: Predation  | Total fish biomass | g/500m$^2$ | The summed biomass of all reef associated non-cryptic fishes observed per 50 x 10 m belt transects at each sampling site, excluding planktivores. | RLS |
| H1: Predation  | Cryptic fish abundance | Individuals/ 100m$^2$ | Count of cryptic fishes observed per 50 x 2 m belt transect at each sampling site. | RLS |
| H2: Resources  | Chlorophyll-a | mg/m$^3$ | Mean chlorophyll-a concentration per sampling site. | Bio-ORACLE |
| H2: Resources  H4: Environment  | Mean SST | °C | Mean sea surface temperature for each site from year 2017. | Bio-ORACLE |
| H2: Resources  | Epiphyte load | g | Wet weight of epiphytes growing on sampled microhabitat. | Sampling |
| H2: Resources  | Depth | m | Depth at which sample was collected. | Sampling |
| H3a: Microhabitat  | Microhabitat | 21 categories | Structurally and taxonomically defined benthic microhabitats, based on the CATAMI scheme (Althaus et al. 2015). See | Sampling |

| | | | | |
|---|---|---|---|---|
| | | | Fraser et al. (2020c) (Chapter 3) for details. | |
| H3b: Habitat group  | Habitat group | 4 categories | Groups of structurally and taxonomically similar microhabitats: macroalgae, live coral, sessile invertebrates (sponges and soft corals), and turfing algae. See Fraser et al. (2020c) (Chapter 3) for details. | Sampling |
| H3a: Microhabitat  H3b: Habitat group  | Branching | Levels 1 – 9 | Microhabitat degree of branching; complexity metric following (Edgar 1983); analogy derived from stream classification (Horton 1945): order of the primary axis, whenever an axis splits the order increases by one. | Sampling |
| H3a: Microhabitat  H3b: Habitat group  | Maximum length | cm | Maximum length of sampled microhabitat from base to distal tip. | Sampling |
| H4: Environment  | Wave exposure | Levels 1 – 4 | Categorical estimate of exposure to wave energy. | Sampling |

| | | | | |
|---|---|---|---|---|
| H4: Environment  | Relief | Levels 1 – 4 | Categorical estimate of vertical relief of the reef site. | Sampling |
| H4: Environment  | Slope | Levels 1 – 4 | Categorical estimate of the steepness of the reef slope. | Sampling |
| H4: Environment  | Currents | Levels 1 – 4 | Categorical estimate of the severity of ocean currents at the site. | Sampling |
| H5: Spatial  | Latitude | °South | Latitude coordinate of sampling site. | Sampling |
| H5: Spatial  | Longitude | °East | Longitude coordinate of sampling site. | Sampling |
| H6: Human impacts  | Human population density | Number of people/km$^2$ | Population density from year 2015. | GPWv4 |

**Table 5.3 (S1)** The hypotheses (epifaunal community temperature-dependent productivity is predominantly driven by: H1 – H6) and linear models tested to explain variation in epifaunal temperature-dependent productivity, with predictions (P) included within models. Partial $R^2$ indicates the proportion of variance explained by each predictor within models; multiple $R^2$ indicates the raw unadjusted $R^2$ for each model. Model selection was based on the Akaike weight, which describes the relative likelihood of each model given the set of candidate models.

| **Hypothesis (H)** | **Model and Predictions (P)** | **Partial $R^2$** | **Multiple $R^2$** | **Akaike weight** |
|---|---|---|---|---|
| **H1 –Predation pressure**  | **PREDATION MODEL** | | 0.018 | <0.01 |
| | P1 – Productivity declines with increased total fish biomass | 0.003 | | |
| | P2 – Productivity declines with increased cryptic fish abundance | 0.015 | | |
| **H2 – Resource availability**  | **RESOURCE MODEL** | | 0.085 | <0.01 |
| | P3 – Productivity declines as depth increases (reducing light) | 0.011 | | |
| | P4 – Productivity increases with epiphyte load | 0.045 | | |
| | P5 – Productivity increases with chlorophyll-a | 0.002 | | |
| | P6 – Productivity increases with mean SST | 0.032 | | |
| **H3a – Characteristics of immediate habitat, fine microhabitat scale** | **MICROHABITAT MODEL** | | 0.588 | 0.08 |
| | P7 – Productivity varies significantly among microhabitats | 0.544 | | |
| | P8 – Productivity increases with habitat branching/complexity | 0.023 | | |

| | | | | |
|---|---|---|---|---|
|  | P9 – Productivity increases with the maximum length of habitat | 0.021 | | |
| **H3b – Characteristics of immediate habitat, coarse habitat group scale**  | **HABITAT GROUP MODEL** | | 0.450 | 0.92 |
| | P10 – Productivity varies significantly among habitat groups | 0.344 | | |
| | P11 – Productivity increases with habitat branching/complexity | 0.030 | | |
| | P12 – The effect of branching on productivity varies among habitat groups | 0.069 | | |
| | P13 – Productivity increases with the maximum length of habitat | 0.007 | | |
| **H4 – Local environmental factors**  | **ENVIRONMENT MODEL** | | 0.074 | <0.01 |
| | P6 – Productivity increases with mean SST | 0.035 | | |
| | P14 – Productivity declines with increased wave exposure | 0.024 | | |
| | P15 – Productivity declines with increased relief | 0.004 | | |
| | P16 – Productivity declines with increased slope | 0.009 | | |
| | P17 – Productivity declines with increased current strength | 0.002 | | |
| **H5 – Geographic location**  | **SPATIAL MODEL** | | 0.036 | <0.01 |
| | P18 – Productivity declines towards higher latitudes | 0.021 | | |
| | P19 – Productivity varies significantly with longitude | 0.015 | | |
| **H6 – Human population impacts**  | **HUMAN IMPACTS MODEL** | | 0.042 | <0.01 |
| | P20 – Productivity increases with human population density | 0.042 | | |

**Table 5.4 (S2)** ANOVA table assessing differences in $P_{20}$ among predictor variables included in each model.

| Source of variation | Degrees of freedom | Sum of squares | *F*-value | *P*-value |
|---|---|---|---|---|
| **Predation model** | | | | |
| Total fish biomass | 1 | 0.06 | 0.53 | 0.470 |
| Cryptic fish abundance | 1 | 0.37 | 3.40 | 0.070 |
| Residuals | 112 | 12.2 | | |
| **Resource model** | | | | |
| Depth | 1 | 0.42 | 4.12 | <0.05 |
| Epiphyte load | 1 | 0.54 | 5.35 | <0.05 |
| Chlorophyll-a | 1 | 0.01 | 0.13 | 0.724 |
| Mean SST | 1 | 0.44 | 4.39 | <0.05 |
| Residuals | 110 | 11.12 | | |
| **Microhabitat model** | | | | |
| Microhabitat | 20 | 7.06 | 6.32 | <0.001 |
| Degree of branching | 1 | 0.25 | 4.42 | <0.05 |
| Maximum microhabitat length | 1 | 0.54 | 9.67 | <0.01 |
| Residuals | 92 | 5.14 | | |
| **Habitat group model** | | | | |
| Habitat group | 3 | 4.37 | 19.4 | <0.001 |
| Degree of branching | 1 | 0.36 | 6.30 | <0.05 |
| Degree of branching x Habitat group | 3 | 0.87 | 3.31 | <0.05 |
| Maximum microhabitat length | 1 | 0.15 | 2.33 | 0.130 |
| Residuals | 106 | 6.96 | | |
| **Environment model** | | | | |
| Mean SST | 1 | 0.68 | 6.63 | <0.05 |
| Wave exposure | 1 | 0.76 | 7.37 | <0.01 |

| | | | | |
|---|---|---|---|---|
| Relief | 1 | 0.04 | 0.39 | 0.531 |
| Slope | 1 | 0.01 | 0.13 | 0.712 |
| Current strength | 1 | 0.01 | 0.06 | 0.809 |
| Residuals | 109 | 11.2 | | |
| **Spatial model** | | | | |
| Latitude | 1 | 0.92 | 8.92 | <0.01 |
| Longitude | 1 | 0.71 | 6.91 | <0.01 |
| Residuals | 112 | | | |
| **Human impacts model** | | | | |
| Human population density | 1 | 0.97 | 9.39 | <0.01 |
| Residuals | 113 | 11.7 | | |

# Chapter 5

# GENERAL DISCUSSION

This thesis presented an ecological investigation into the potential interactions between local- and broad-scale drivers of variation in assemblages of small mobile epifaunal invertebrates inhabiting shallow reefs. Samples of diverse, common reef microhabitats and associated epifauna were collected along a latitudinal gradient from southern Tasmania to the northern Great Barrier Reef, representing extensive climatic, environmental and biogeographic gradients. Overwhelmingly, variation in epifaunal assemblages was best explained by differentiating samples according to habitat type, with any latitudinal patterns emerging only via interactions with habitat.

The majority of ecological research involving epifaunal invertebrates has focussed on relationships between assemblages and their immediate habitat (Hacker and Steneck 1990, Gee and Warwick 1994a, Taylor 1997, Chemello and Milazzo 2002, Stella et al. 2010, Kramer et al. 2014, Marzinelli et al. 2014, Stelling-Wood et al. 2020). In this context, the clear associations with habitat presented in the previous chapters are unsurprising. The novelty of the research presented in my thesis lies in the variety of habitats sampled, and in the broad latitudinal gradient across which sampling was conducted, covering both rocky and coral reefs and a diversity of environmental and ecological conditions. To date, no published research has investigated epifaunal ecology across such a substantial biogeographic range, using consistent sampling techniques to quantify assemblages associated with 21 structurally and taxonomically diverse microhabitats. The consistently strong associations with habitat, especially at the coarse level of classification into four broad habitat groups, substantially advances knowledge in this field. The distinct lack of overarching latitudinal patterns also

provides a valuable contribution to this field of research, suggesting knowledge of habitat alone should facilitate accurate predictions of variation in this basal trophic group in response to local anthropogenic and broader ocean-warming pressures.

Epifaunal assemblages are difficult to sample in the field, and quantifying assemblage metrics requires technical, laborious, and time consuming (thus, expensive) laboratory processing. In contrast, assessments of benthic habitat availability via visual approaches such as SCUBA-based surveys or photographic and videographic techniques are much more efficient. The results presented in my thesis suggest that, where resources and/or expertise are limited, key properties of epifaunal assemblages can be estimated at broad scales using data obtained from efficient benthic habitat surveys.

## Consistency across broad biogeographic scales

The lack of an independent latitudinal effect was largely unexpected, given clear latitudinal patterns in other ecosystem processes. Substantial effects of temperature and latitude have been observed in forests (Gillman et al. 2015), open oceans (Petersen and Curtis 1980), freshwater streams (Patrick et al. 2019), and seagrass beds (Duarte and Chiscano 1999). Examples from reef systems include latitudinal patterns in the biomass and species richness of coral reef fishes and large invertebrates (Duffy et al. 2016, Stuart-Smith et al. 2018), latitudinal variation the effect of coral bleaching on functional richness and species richness of fishes and large invertebrate (Stuart-Smith et al. 2018), and the diversity, density and biomass of herbivorous fishes (Floeter et al. 2005).

Any latitudinal patterns of variation within communities of small invertebrates appear inconsistent among previous studies. Virnstein et al. (1984) described latitude as “an inconsistent predictor of differences in structure of the epifaunal component of seagrass communities”. Edgar (1993) found constant productivity of epifaunal assemblages on

uniform artificial habitats among 17 heterogenous sites worldwide. Recently, Mazurkiewicz et al. (2020) reported latitudinally consistent biomass size-spectra of soft-sediment infauna in northern hemisphere fjords. In contrast, Kramer et al. (2017) presented the most thorough recent investigation of latitudinal patterns in reef-associated epifauna, and identified clear tropical/temperate differences. Their study was conducted by sampling microhabitats of similar structural complexity from one tropical and one temperate reef location and comparing associated assemblages of small crustaceans. Kramer et al. (2017) identified distinct tropical and temperate assemblages, and clear variation among habitats of different complexity. Given these results, I expected an independent latitudinal pattern and clear latitudinal variation on habitats of similar structure. While I did observe latitudinal variation in the epifaunal size spectrum on some habitats (Chapter 3), there were no overarching patterns in my data purely relating to the latitudinal gradient.

## Caveats and future directions

Latitudinal patterns may be more clearly apparent if species-level identification had been performed. Species composition was not included and, although major orders and families are consistent across eastern Australia, taxonomic research suggests species are likely to vary (Lowry and Springthorpe 2007, Myers and Lowry 2009). Species-level identification is difficult due to the immense diversity of assemblages, the small size of the animals, the need for accurate keys and/or dissection (Guerra-Garcia and Takeuchi 2004), and the fact that a large proportion of species have not yet been described (Nakaoka et al. 2001). If taxonomic expertise is available, future research into the relationship between latitude and the species, or morphospecies, composition of these assemblages may facilitate more accurate understanding of variation with latitude and predictions of shifts with ocean warming.

Taxonomic diversity and richness are recognised as important indicators of ecosystem health that are often highly correlated with other faunal metrics such as productivity (Duffy et al. 2017), however diversity and richness metrics were not considered here. This was primarily because taxonomic resolution was inconsistent between macro- and meiofauna (macrofauna ≥1mm were identified to family; meiofauna <1mm were identified to order) and a total of only 33 orders were identified across the entire dataset. Hence, estimates of taxonomic diversity and richness would be largely meaningless.

Given the strength of the habitat effect observed here, any patterns in diversity or richness are likely to be primarily mediated via the effect of habitat. However, clear latitudinal gradients in diversity are recognised in many ecosystems, with tropical regions typically supporting higher taxonomic diversity than temperate zones (Rohde 1992, Clarke and Crame 1997, Attrill et al. 2001, Hillebrand 2004). Previous studies of epifaunal diversity indicate similar latitudinal patterns (Virnstein et al. 1984, Jablonski et al. 2000). Given the strong correlation between diversity and a range of ecological functions observed in other trophic groups (Gillman et al. 2015, Duffy et al. 2017), assessing the potential interactions between habitat effects and latitudinal gradients in the diversity of reef-associated epifauna may further clarify drivers of the fuel this basal trophic group provides to shallow reef food webs.

Another interesting aspect of faunal assemblage composition and diversity is the functional role of individuals within the assemblage. Functional composition and diversity are increasingly acknowledged as primary drivers of ecosystem function (Stuart-Smith et al. 2013, Stuart-Smith et al. 2015). In fact, community functional diversity is often a better predictor than species richness for a majority of ecosystem properties, including biomass across trophic groups within complex food webs (Lefcheck and Duffy 2015). Epifaunal assemblages comprise a diversity of functional groups, including herbivores, detritivores, filter-feeders, and carnivores (Edgar 1993, Poore et al. 2012). Our understanding of the

contribution of this important trophic group to reef food webs under different environmental and ecological conditions can be greatly improved through further assessment of variation in functional composition and diversity.

In this thesis, I have not directly investigated potential mechanisms driving the strong correlations between epifaunal assemblages and their immediate habitat. Epifaunal variation among habitats was likely driven by a combination of top-down (consumer pressure) and bottom-up (resource supply) trophic control, as well as intra-assemblage competition for space (Chapters 3, 4, 5). However, covariates estimating site-scale consumer pressure and food resource availability did not significantly correlate with epifaunal productivity (Chapter 5). In fact, no site- or regional-scale covariates were useful for explaining variation in epifaunal productivity, suggesting that the spatial scale at which potential covariates are compared is a critical consideration (Dayton and Tegner 1984).

Habitat structure was quantified at the centimetre scale, which is much closer to the scale at which the local environment is perceived and partitioned by epifaunal invertebrates than the metre or kilometre scale of site- or regional-scale covariates. Mesocosm experiments (Edgar and Aoki 1993) in which predators are excluded from a diversity of habitat types that offer a quantified diversity of food resources may clarify the relative roles of top-down and bottom-up control among habitats. The influence of space, competition and habitat partitioning in driving the strong assemblage-habitat associations may by clarified by more accurate quantification of the spatial niches available among, and utilised within, microhabitats by epifaunal assemblages (Brandl et al. 2015). Approaches such as the use of fractal geometry techniques that relate specifically to the scale at which habitat structure might be perceived by the size of resident animals (Gee and Warwick 1994b) should be useful for future investigations aimed at assessing the extent that different mechanisms drive the strong habitat associations of epifaunal assemblages observed here.

## Ecological implications

### Habitat transformation

Overall, this research suggests that ocean-warming and local anthropogenic stressors will change the community structure of epifauna on shallow reefs, however these changes will almost exclusively relate to shifts in benthic habitat availability. Interestingly, the three habitat extremes identified in terms of the taxonomic and size structure, as well as the productivity of epifaunal assemblages (live hard coral, macroalgae, and turfing algae) (Chapters 2, 3, 5), also represent three habitat extremes in observations of reef transformation, degradation, or 'collapse' on a global scale. Both coral- and macroalgae-reefs are 'collapsing' towards turf-dominated states (Filbee-Dexter and Wernberg 2018, O'Brien and Scheibling 2018, Reeves et al. 2018). The results presented in the preceding chapters imply that if the 'collapse' of reefs continues to a point where turfing algae becomes the dominant benthic habitat type, a prolific epifaunal community will still exist, maintaining a major source of food and energy for reef food webs.

The magnitude and nature of shifts within the epifaunal trophic resource will depend on whether habitat is transforming from coral to turf, or from macroalgae to turf (or indeed from coral to macroalgae or vice versa (Mumby et al. 2007b, Ling et al. 2018a)). Coral reef epifauna will change dramatically with a shift towards turf-dominance, losing characteristic large decapods and gaining high densities of small harpacticoid copepods (Chapters 3, 4). In fact, the overall density, biomass and productivity of epifaunal invertebrates on tropical coral reefs dominated by dead turf-covered coral will be greater than on reefs dominated by healthy corals (Chapter 4), albeit with much of this transformation channelled through extremely small animals. In contrast, collapse of macroalgae on temperate reefs towards turf-dominance will result in less dramatic change in epifauna, with a slight steepening of the size spectrum

as some larger peracarids are lost and small harpacticoid copepods are gained, and larger size classes within the assemblage will become dominated by non-crustacean taxa (Chapter 3). The overall total productivity of epifauna is not likely to change greatly between macroalgae and turfing algae (Chapter 5).

**Timeframes of reef collapse**

Changes predicted above will nevertheless depend on the timeframe of reef degradation. On tropical reefs, dead skeletons of branching coral will eventually degrade through coral rubble to sand (Enochs and Manzello 2012), supporting invertebrate communities of lower density, biomass and productivity (Kramer et al. 2014, Nelson et al. 2016). Without adequate recruitment of live corals to replenish dead coral and coral rubble, it is reasonable to expect longer-term declines in the basal epifaunal food resource on tropical reefs. The calcium carbonate reef structure will likely persist over a longer timeframe than branching coral skeletons (Kleypas and Yates 2009), providing substrate for turfing algae and, hence, maintaining useful habitat for a productive epifaunal assemblage. A potential quandary with this assumption is the issue of ocean acidification. If ocean pH continues to drop, the calcium carbonate reef structure will ultimately dissolve until little remains to support turfing algae (or macroalgae) (Kleypas and Yates 2009). In contrast, rocky reef substrates are more resistant to ocean acidification and the physical processes eroding coral reefs (Leisten 2002), and are thus likely to persist longer term.

The availability of turfing or macroalgae habitat for epifauna on many rocky reefs also depends on the density of herbivorous sea urchins (Ling et al. 2015). Herbivorous urchins have the capacity to graze rocky reefs until only bare rock remains, creating phenomena known as ‘urchin barrens’ that support minimal epifaunal invertebrates (Ling 2008). Ocean acidification may facilitate the persistence or recovery of non-calcareous algae on rocky reefs

as the carbonate structures of sea urchins are vulnerable to decreased pH (Asnaghi et al. 2013). However, some small invertebrates have calcareous body structures, so epifaunal assemblages may also change dramatically under conditions of decreased pH, regardless of habitat availability (Kroeker et al. 2011).

**Implications for subtropical reefs**

Although analyses presented here tend to separate sampling locations into 'tropical' and 'temperate' biomes, unique subtropical reefs exist adjacent to Australia's east coast that are also experiencing dramatic transformation. These subtropical reefs represent a thermal tolerance limit for a wide array of taxa, including species of coral and macroalgae (Harriott and Banks 2002, Edgar 2008). Both Elizabeth and Middleton Reefs and the Solitary Islands are subtropical (latitude approximately 30° S). Elizabeth and Middleton Reefs are atolls formed by coral accretion (Kennedy and Woodroffe 2004). In contrast, the Solitary Islands' reefs are generally not accreting, rather corals attach to rocky substrata (Veron et al. 1974, Dalton and Roff 2013).

While this thesis did not explicitly discuss changes to epifauna on subtropical reefs, results suggest that changes are likely to depend almost entirely on how reef habitats transform. Currently, subtropical live coral-associated epifaunal assemblages are statistically similar to live coral assemblages from tropical reefs (Chapter 4), and the same applies to macroalgae-associated assemblages on subtropical and temperate reefs (Chapters 2, 3, 5). However, tropical and temperate macroalgae host significantly different epifaunal assemblages in terms of size structure (Chapter 3). If subtropical reefs become warmer and more tropical, as predicted (Kim et al. 2019), macroalgae species already at their northern limits may decline and the size spectra of epifaunal assemblages inhabiting the remaining macroalgae may steepen with more copepods, while the relatively high density of large peracarids may be

replaced by few large decapods (Chapter 3). If tropical coral species can extend their range into subtropical latitudes, or recruitment increases on subtropical reefs (Price et al. 2019), little change may be expected in coral-associated epifaunal assemblages. Alternatively, if tropical coral species cannot recruit effectively to subtropical reefs, and subtropical corals continue to decline with coral bleaching and other stressors (Kim et al. 2019), turfing algae and/or macroalgae may become the dominant benthic habitat. In this case, associated epifaunal assemblages will likely be more productive than those on existing subtropical coral habitats (Chapter 4), with steeper size spectra dominated by harpacticoid copepods and lacking the characteristic large decapods of live coral (Chapter 3, 4).

**Conclusions**

Global climate change, combined with myriad local stressors, is expected to continue driving dramatic shifts in shallow reef ecosystems. The results presented in this thesis imply that any resulting shifts at basal reef food web levels (i.e. epifaunal invertebrates) will be mediated almost exclusively via changes in benthic habitats. Habitat variation, at the spatial scale of a single macroalgae thalli or fragment of a branching coral head, consistently exceeded all other environmental or ecological covariates in explaining variation in epifaunal assemblages, regardless of which assemblage metric was used. Epifaunal assemblage properties were highly predictable according to habitat characteristics, suggesting accurate prediction of basal epifaunal food resources within shallow reef food webs is possible with knowledge of benthic habitat availability. This research provides critical information for predicting energy flow throughout reef food webs on changing reefs, thus facilitating improved management practices for maintaining ongoing trophic functions of reef systems.

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